Spring–mass behavior and electromyographic activity evolution during a cycle-run test to exhaustion in triathletes

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ABSTRACT

Purpose: To evaluate spring–mass (SM) behavior and associated electromyographic (EMG) activity during a run to exhaustion following a cycle exercise in trained triathletes.
Methods: Ten triathletes completed four tests: a cycling test to determine $\dot{V}O_{2max}$; a running test to determine the lactate threshold (LT); a 5 min control run at LT (C-Run) followed after a total recovery period by a cycle-to-run session to exhaustion [30 min of cycling at $\sim$80% $\dot{V}O_{2max}$ followed by a run until exhaustion at LT (T-Run)]. SM behavior and EMG signals in nine lower limb muscles were recorded throughout the running sessions.
Results: Immediately after cycling, leg stiffness was 12.1% higher than its C-Run value and a concomitant increase of EMG activity of knee extensors was observed during pre-contact. Throughout T-Run, leg stiffness decreased by 7.3%, while knee extensors and ankle flexors activities decreased during pre-contact and braking phases. No significant variations in SM parameters and no significant increase of muscle activity were reported between C-Run and the end of T-Run.
Conclusion: SM behavior during the cycle-run test was consistent with EMG activity changes. Cessation of exercise was not associated with significant alterations of stiffness values and EMG activity.

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1. Introduction

Triathlon is a complex sport that involves sequential swimming, cycling, and running over a variety of distances [i.e., from sprint distance (750-m swim, 20-km cycle, and 5-km run) to long distance (3.8-km swim, 180-km cycle, and 42-km run)]. This sport requires the ability to excel at and to link three separate disciplines, but recent studies have demonstrated that the outcome of the race is mainly associated with the running performance (Le Meur et al., 2009, 2011). Le Meur et al. (2011) showed that top triathletes revealed less running speed variability than other competitors in the field by maintaining their initial pace for a longer time during an international competition. This finding suggested that running performance during a triathlon might be linked with the ability to resist fatigue (Le Meur et al., 2011). Parameters influencing a decrease in running speed during a triathlon have been widely studied from a metabolic point of view (Hausswirth and Brisswalter,

2008), but additional understanding of mechanical modifications occurring with fatigue continues to be a challenge to improve our understanding of performance factors, and to develop optimized training programs in triathlon.

Running has often been described as a bouncing locomotion pattern in which the running leg functions similarly to a linear spring. The mass–spring model introduced by McMahon and Cheng (1990) involves relatively simple modeling of the running leg based on ground reaction force and center of mass displacement characteristics. Despite its relative simplicity, this model has contributed to better understanding of running mechanics (Dutto and Smith, 2002; Farley and Gonzalez, 1996; Hunter and Smith, 2007; Rabita et al., 2011). The model consists of a point mass supported by a single massless linear "leg spring". The main parameter studied when using spring–mass model is the stiffness of the leg spring (k_{leg}), defined as the ratio of the maximal vertical force to the maximum leg compression (Farley and Gonzalez, 1996). Moreover, although it does not correspond to any physical spring, the vertical stiffness (k_{vert}) is used to model the vertical motion of the center mass during contact (Farley and Gonzalez, 1996; McMahon et al., 1987). It is defined as the ratio of the maximal force to the vertical downward maximal displacement

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of the CM as it reaches the lowest point. Recently, the spring–mass model was employed to analyze the biomechanical behavior of elite triathletes performing a running time-to-exhaustion at 95% of the velocity associated with $\dot{V}O_{2max}$ (Rabita et al., 2011). Rabita et al. (2011) reported that k_{leg} decreased by 13% between the beginning and the end of the test. This finding was associated with a significant decrease in the maximal vertical force, while no significant variation was observed for leg compression. Interestingly, k_{vert} remained unchanged during the same period of time. The subjects compensated the fatigue-induced impairment of the neuromuscular function of force production by increasing leg-spring angle. Alterations of vertical forces were related with the decrease of the angle of velocity vector at toe off ($r^2 = 0.73$). By this way, the decrease in the velocity vector angle at takeoff allowed them to flatten the trajectory of the center of mass. The increase in the leg-spring angle at the moment of impact allowed the subject to maintain constant horizontal impulse, which contributed to the maintenance of constant velocity during later stages of the run. To the best of our knowledge, this experiment remains the only one performed with triathletes, and no study has ever investigated the time course of the SMM in the context of triathlon, where the running performance is achieved after the completion of a demanding cycling leg. Considering that cycling is likely to affect both metabolic (Hausswirth et al., 1997) and neuromuscular responses (Lepers et al., 2001, 2008) during the subsequent run, further investigation is required to characterize spring–mass behavior in this particular context.

Some studies have suggested that the leg-spring behavior during maximal exercise is related to changes in the neuromuscular function occurring during the task. This assumption was supported by EMG studies investigating the effect of fatigue during running (Nummela et al., 2006, 2008) or jumping exercises (Horita et al., 2002; Kuitunen et al., 2007). Horita et al. (2002) have found that in drop jump exercise, *vastus lateralis* pre-activation correlated with knee stiffness during the initial phase of contact, suggesting that leg stiffness might be dependent of muscle recruitment during the pre-contact phase. Only one study investigated the time course of EMG activity throughout a maximal long-duration run (10 km) (Paavolainen et al., 1999), during which the subjects had to complete a constant velocity 200 m lap five times during the course of the run. This study reported a lack of significant change in four leg muscles activity (*vastus lateralis*, *biceps femoris*, *gastrocnemius lateralis* and *rectus femoris*), despite a significant decrease of ground reaction forces was observed during the running laps performed at a constant velocity. This finding led the authors to postulate that a neuromuscular fatigue phenomenon took place during the test, but further studies are still required to confirm this hypothesis for maximal running tests of similar duration. In the particular context of the triathlon run, several studies investigated the influence of cycling on muscle recruitment during subsequent running (Bonacci et al., 2010; Chapman et al., 2008; Heiden and Burnett, 2003) and reported heterogeneous results. While changes in muscle activation in trained triathletes were observed by Heiden and Burnett (2003), Chapman et al. (2008) and Bonacci et al. (2011) showed that cycling did not adversely influence neuromuscular control in elite triathletes during the triathlon run. Nevertheless, these three studies imposed lower intensity rather than competition, and focused on the time course of the EMG activity only during the initial phase of the run. Taken together, these results suggested that further investigations are required to characterize the influence of cycling on EMG activity during the triathlon run to better understand its possible influence on running mechanics.

The major aim of this study was to characterize changes in SMM behavior in trained triathletes throughout an exhaustive run performed after an intense cycling exercise (i.e., triathlon run). After this first step, the second goal was to identify whether potential changes were consistent with modifications of EMG activity of lower limb muscles during the fatiguing run. We hypothesized that leg stiffness would decrease with the onset of fatigue throughout a triathlon run performed until exhaustion and that would be accompanied by modifications in the neuromuscular control of knee and ankle extensors.

2. Materials and methods

The experiment was performed between April and May, just prior to the competition period. Ten well-trained triathletes gave their written informed consent to participate in this investigation, which was conducted according to the Declaration of Helsinki. Selection was based on the athlete's best performance over a short distance triathlon (1.5 km swim, 40 km cycling, 10 km run) during the past year (mean time of 2 h 15 min ± 5 min). The athletes had cycled 202 ± 30 km and run 39 ± 12 km per week, during the previous 4 months. A local ethics committee for the protection of individuals gave approval concerning the project before its initiation. The triathletes were informed of the possible risk and discomfort associated with the experimental procedures before they gave their written consent.

2.1. Exercise protocol

The participants had three laboratory test sessions within a 15-days period. During the entire experimental procedure, they did not perform any exhausting exercise in the 48 h preceding each test.

2.1.1. Maximal cycling test

Each subject performed incremental cycling on an electronically braked cycle ergometer (Excalibur Sport, Lode®, Groningen, The Netherlands) equipped with standard 170-mm cranks. Vertical and horizontal positions of the saddle, handlebar height, and stem length were set to match the usual dropped posture, racing position of the participants with the torso partially to fully bent-over, hands on the drops portion of the handlebars and elbows partially flexed (elbow angle less than 160°).

The test was performed until complete exhaustion to estimate maximum oxygen uptake ($\dot{V}O_{2max}$), maximal aerobic power (MAP), and power output associated with ventilatory thresholds. This incremental session began with a warm-up at 100 W for 6 min, after which the power output was increased by 30 W/min until volitional exhaustion. Heart rate (HR), oxygen uptake ($\dot{V}O_2$), oxygen equivalent ($\dot{V}_E/\dot{V}O_2$), and carbon dioxide equivalent ($\dot{V}_E/\dot{V}CO_2$) values were continuously recorded breath-by-breath using a telemetric system collecting gas exchanges (Cosmed K4b^2, Rome, Italy). All of these data were subsequently averaged every 15 s. $\dot{V}O_{2max}$ was determined according to criteria described by Howley et al. (1995); a plateau in $\dot{V}O_2$ despite an increase in power output, a 1.15 respiratory exchange ratio, or an HR over 90% of the predicted maximum HR (Table 1). The mean value of the last minute of the test determined the maximal power tolerated. The first and second ventilatory thresholds (VT1 and VT2, respectively) were determined according to criteria previously described by Beaver et al. (1986) to calculate the appropriate workload imposed by the cycle ergometer for the cycle-to-run combination test.

2.1.2. Incremental running test

This test was performed on a motorized treadmill, whose speed was controlled with a custom-made optical device. The device consisted of an infrared sensor connected to a USB data acquisition board (DT9800, Data Translation, Marlboro, MA, USA) and reflectors evenly spaced on the treadmill strip. The signal was continuously

Table 1
Anthropometrical and physiological characteristics of the triathletes ($n = 10$).

Parameters		Men
Age (years)		30 ± 6
Weight (kg)		68.4 ± 7.4
Height (cm)		175 ± 4
Cycling	$\dot{V}O_{2max}$ (mlO$_2$ min^{-1} kg^{-1})	63.0 ± 4.3
	MAP (W)	347 ± 29
	P_{VT1} (W)	219 ± 24
	P_{VT1} (%$\dot{V}O_{2max}$)	70.6 ± 5.0
	P_{VT2} (W)	280 ± 30
	P_{VT2} (%$\dot{V}O_{2max}$)	87.7 ± 4.9
Running	$\dot{V}O_{2max}$ (mlO min^{-1} kg^{-1})	61.6 ± 3.7
	Maximal speed sustained (km h^{-1})	18.5 ± 0.7
	V_{LT} (km h^{-1})	15.7 ± 0.6
	V_{LT} (%$\dot{V}O_{2max}$)	86.9 ± 4.6

$\dot{V}O_{2max}$: maximal oxygen uptake, MAP: Maximal aerobic power, P_{VT1}: Power output at the first ventilatory threshold, P_{VT2}: Power output at the second ventilatory threshold, V_{LT}: running speed at the lactate threshold.

recorded at a 1-kHz sampling frequency and processed in real time, so that treadmill speed was displayed on a PC screen with a 0.1 km h^{-1} accuracy (Testpoint software, Measurement Computing Corp., Norton, MA, USA).

The test began at 12 km h^{-1} with a 0% grade, and the speed was increased by 1 km h^{-1} every 3 min until volitional exhaustion. Subjects were required to maintain the same position on the treadmill using a rope tied at waist level. The horizontal forces induced by this rope were negligible, because it was highly elastic. Between each increment, there was a 30 s rest period to collect capillary blood samples from the ear lobes. Blood lactate was analyzed using the Lactate Pro system. Lactate threshold (LT) was then assessed according to the D-max method previously described by Cheng et al. (1992), and $\dot{V}O_2$ max was determined according to the same criteria as the cycling maximal test (Howley et al., 1995).

2.1.3. Control run (C-Run) and maximal cycle-to-run combination test

The subjects warmed-up during a 20 min run on a treadmill (i.e., 15 min at 11 km h^{-1}, 5 min at 13 km h^{-1}). This warm-up session was followed by a 5 min recovery period. Then, the subjects were told to run for 5 min at LT (C-Run) (Fig. 1).

After a 10-min passive recovery period, the subjects were told to cycle for 10 min at 150 W to ensure a complete recovery. For all triathletes, [La$^-$]$_b$ value dropped out under 2 mmol L^{-1} after this period. Then, they were asked to perform a cycle-to-run combination consisting of 30 min at a mean intensity Δ50% between VT1 and VT2, followed by running to fatigue at LT (T-Run). According to previous studies on the effect of a cycling event on subsequent running adaptation (Bernard et al., 2003; Hue et al., 1998; Lepers et al., 2008), this workload was representative of a sprint distance triathlon (750-m swim, 20-km cycle, and 5-km run). The cycling bout was conducted on a cycle-ergometer, which allowed the athletes to maintain constant power output independently of cycling

cadence. Cycling cadence was left free throughout the test. To ensure that the subjects gave their best effort, they were verbally encouraged throughout T-Run to continue as long as possible. The mean (SD) transition time between the cycling and running events (76 ± 14 s) was the same as that within an actual competition (Le Meur et al., 2009).

2.2. Spring–mass model characteristics

In order to measure stride temporal characteristics during T-Run, i.e., contact time (t_c in s), flight time (t_f in s), and step frequency (SF in Hz), two contact-sensing resistors (Interlink Electronics, Camarillo, CA, USA) were taped under the sockliner of the right shoe, facing the heel and the base of the first metatarsus, according to the recommendations of Morin et al. (2005). Data were sampled at 1000 Hz and recorded via a portable data logger device (ME6000, Mega Electronics Ltd., Kuopio, Finland). This method allowed the detection of the instants of heel-strike and toe-off and thus measurement of t_c and t_f for each step, in field conditions.

The main mechanical parameters of the SMM were calculated for each step and averaged over 30 consecutives strides, according to a validated method based on a sine-wave modeling of the force–time curve during contact (Morin et al., 2005). From the basis modeling of $F(t)$ curves by a simple sinus function, vertical stiffness (k_{vert} in kN m^{-1}) was calculated as the ratio of maximal force (F_{max} in kN) to the maximal downward displacement of the center of mass during contact (Δy_c in m):

$$K_{vert} = F_{max}.\Delta y_c^{-1}$$

with

$$F_{max} = m \cdot g \cdot \frac{\pi}{2} \cdot (t_f/t_c + 1)$$

m being the subject's body mass (in kg), and

$$\Delta y_c = F_{max} \cdot \frac{t_c^2}{m \cdot \pi_2} + g\frac{t_c^2}{8}$$

Leg stiffness (k_{leg} in kN m^{-1}) was calculated as the ratio of F_{max} to the peak displacement of the leg spring ΔL (in m) during contact:

$$k_{leg} = F_{max}.\Delta L^{-1}$$

with

$$\Delta L = L - \sqrt{\left(L^2 - \left(\frac{v^2 \cdot t_c^2}{2}\right)\right)^2} + \Delta y_c$$

assuming that the peak downward displacement of the center of mass occurs at the moment F_{max} is reached (Farley and Gonzalez, 1996). In this equation, v is the mean forward velocity of the body imposed by the treadmill (in m s^{-1}), and t_c is the ground contact time at each step. The subject initial leg length (L) was determined
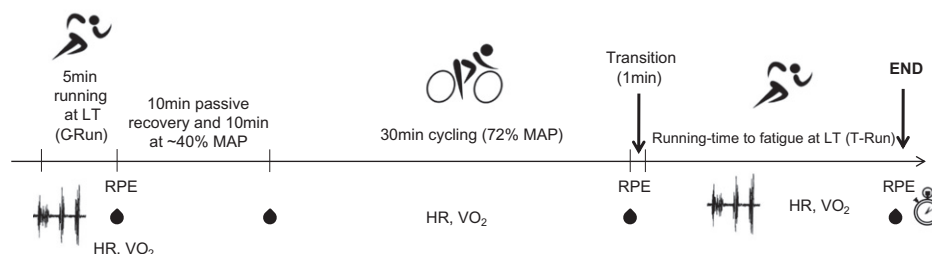
Fig. 1. Graphic representation of the experimental protocol. MAP: maximal aerobic power; HR: heart rate, LT: lactate threshold, RPE: rate of perceived exertion.

by measuring the vertical distance between the central palpable point of the greater trochanter and the ground.

2.3. Assumptions of the sine-wave model

The basis of the model employed to compute stiffness in the present study (Morin et al., 2005) postulates that the $F(t)$ curve can be fitted by means of a simple sine function. As a consequence, it was assumed that leg stiffness, defined as the ratio of the maximal force in the spring to the maximum leg compression, and vertical stiffness, defined as the ratio of the maximal force to the vertical displacement of the CM as it reaches its lowest point, were attained at the middle of the stance phase during constant velocity running.

2.4. Electromyography

The electrical activity of nine muscles of the right lower limb was monitored with pairs of surface Ag/AgCl electrodes (Blue Sensor Q-OO-S, Medicotest S.A.R.L, France). These muscles included: *tibialis anterior* (TA), *soleus* (SOL), *gastrocnemius lateralis* (GaL), *gastrocnemius medialis* (GaM), *vastus lateralis* (VL), *vastus medialis* (VM), *rectus femoris* (RF), *semimembranosus* (SM), and *biceps femoris* (BF). The electrodes were placed longitudinally with respect to the underlying muscle fiber arrangement and located according to the surface EMG for the noninvasive assessment of muscles (SENIAM) recommendations. The wires connected to the electrodes were well secured with tape to avoid movement-induced artifacts. Raw EMG signals were preamplified (with a gain of 375) close to the electrodes, band-pass filtered (8–500 Hz), amplified (ME6000P16; Mega Electronics), and analog-to-digitally converted at a sampling rate of 1 kHz. The same portable data logger device was employed for both kinematic and EMG recording to allow the synchronization of the data.

A high-pass filter (20 Hz) was applied to the raw EMG signals (Chart 5.4, AD Instruments®, Hasting, UK) to eliminate possible movement artifacts. This signal was full-wave-rectified and the root mean square (RMS) was computed with a 20-ms moving window. EMG data were smoothed and then averaged during 30 consecutive strides to get a mean EMG RMS envelope for each muscle. The overall activity was identified by the magnitude of the mean EMG RMS computed with a 20-ms moving window for four phases of the stride: pre-contact phase (100 ms before ground contact) (Komi et al., 1987; Kyrolainen et al., 2001, 2005), braking phase (first half of the ground contact), propulsive phase (second half of the ground contact), and flight time (excluding the pre-contact phase).

2.5. Physiological parameters

$\dot{V}O_2$ and HR were monitored continuously throughout both the C-Run and maximum cycle-to-run test using the same gas analyzer. Blood samples (5 μl) were collected from the earlobe to measure blood lactate concentration ([La⁻]) at the end of both the cycling and running legs.

2.6. Rating of perceived exertion (RPE)

The RPE was measured using the Borg scale (Borg, 1970). This scale measures the overall subjective sensation of effort accompanying the exercise. The scale and what it measured was carefully explained to all subjects before the incremental test and the cycle-to-run test. Subjects were instructed to give a general RPE immediately at the end of the cycling period and just after the completion of the running leg during the cycle-to-run test.

2.7. Data analysis

The ME6000 biomonitor data logger recorded both the FSR sensor and EMG signals, allowing temporal synchronization. Averaged SMM and EMG RMS values were measured at 4 min during C-Run, at 30 s during T-Run (T-Run$_{5\%}$) and at each 20% of T-Run (T-Run$_{20\%}$,...,T-Run$_{100\%}$). The physiological parameters were averaged during the last 30 s of C-Run and T-Run$_{100\%}$ for subsequent analyses.

2.8. Statistical analysis

Statistical analysis was performed using the SPSS 19 package (IBM corporation, Inc., New York, USA). All descriptive statistics presented in the text, tables and figures are mean values ± SD. Since the present protocol involved a relatively small number of subjects and the data obtained did not always meet the assumptions of normality as assessed visually by normal probability plot and by the Shapiro–Wilk test, non-parametric statistical analyses ensued. A Wilcoxon test was performed to analyze the time course of cycling cadence between the first and the last 5 min periods of the cycling leg. Friedman rank test was undertaken to assess the statistical differences between time periods (C-Run, T-Run$_{5\%}$,...T-Run$_{100\%}$) for spring–mass model parameters and EMG RMS values of the nine muscles during the four phases of the stride (pre-contact, braking, propulsive, and flight phases). The cycling effect on these variables was analyzed by comparing C-Run and T-Run$_{5\%}$ values. The time effect during T-Run was investigated by comparing all the values from T-Run$_{20\%}$ to T-Run$_{100\%}$ with C-Run (no fatigue condition) and T-Run$_{5\%}$ (post-cycling condition) ones. When a significant F-value in Friedman's analysis was found, a *post-hoc* test was used to determine the between-means differences. To avoid type I error inflation, the *post-hoc* analysis was performed using Bonferroni correction. For all statistical analyses, a p value of 0.05 was accepted as the level of significance.

3. Results

The results collected during the two maximal incremental tests are presented in Table 1.

3.1. Performance and cycling cadence

The cycling session was achieved at a mean power output of 249 ± 27 W. No significant change of cycling cadence was reported between the first and the last 5 min periods of the cycling session (88 ± 11–88 ± 12 rpm, $p = 0.92$). The running leg of the cycle-run session was performed at a mean speed of 15.7 ± 0.6 km h^{-1} with a mean duration of 15 min 35 s ± 4 min 41 s.

3.2. SMM characteristics

The time course of the SMM parameters is depicted in Table 2. The mean curves of k_{leg} and k_{vert} during T-Run are presented in Fig. 2. SL, SF, k_{vert} and Δy did not elicit significant variations throughout the protocol (i.e. C-Run and T-Run).

3.2.1. C-Run vs. T-Run$_{5\%}$
t_c decreased by 4.6% ($p = 0.01$) and t_f increased by 8.3% ($p = 0.01$) between these two periods. k_{leg} increased by 12.1% (8.99 ± 1.75 vs. 10.08 ± 1.94 kN m^{-1}, for C-Run and T-Run$_{5\%}$, respectively, $p = 0.01$), while higher F_{max} values (+4.8%, $p = 0.01$) and lower ΔL values (−6.9%, $p = 0.01$) were reported at T-Run$_{5\%}$ than during C-Run.

Table 2
Mean (±SE) values of stride spatio-temporal and spring–mass model parameters during the control (C-run) and the transition run to exhaustion (T-Run).

Parameters	C-Run	T-Run$_{5\%}$	T-Run$_{20\%}$	T-Run$_{40\%}$	T-Run$_{60\%}$	T-Run$_{80\%}$	T-Run$_{100\%}$
Stride length (m)	2.95 ± 0.02	2.95 ± 0.03	2.95 ± 0.03	2.95 ± 0.04	2.96 ± 0.04	2.93 ± 0.04	2.96 ± 0.03
Stride frequency (Hz)	1.47 ± 0.01	1.47 ± 0.01	1.47 ± 0.01	1.47 ± 0.02	1.47 ± 0.02	1.48 ± 0.02	1.46 ± 0.02
Contact time (ms)	222 ± 6	211 ± 6**	216 ± 6	216 ± 7	219 ± 7##	219 ± 7##	218 ± 6##
Flight time (ms)	120 ± 5	130 ± 6*	127 ± 6	127 ± 7	124 ± 7	122 ± 8	125 ± 7
k_{leg} (kN m^{-1})	8.99 ± 1.75	10.08 ± 1.94**	9.61 ± 1.80*	9.63 ± 1.93*	9.25 ± 1.92##	9.30 ± 1.96##	9.34 ± 1.77#
k_{vert} (kN m^{-1})	28.88 ± 3.85	30.32 ± 3.96	29.63 ± 3.81	29.72 ± 3.94	29.13 ± 4.06	29.47 ± 4.01	29.16 ± 3.47
F_{max} (kN)	1.67 ± 0.19	1.75 ± 0.21*	1.72 ± 0.20	1.71 ± 0.21	1.69 ± 0.21	1.69 ± 0.22#	1.68 ± 0.21#
ΔL (cm)	18.9 ± 2.0	17.6 ± 1.8**	18.1 ± 1.8	18.1 ± 2.0	18.7 ± 2.1##	18.5 ± 2.1#	18.5 ± 1.8#
Δy (cm)	5.8 ± 0.2	5.8 ± 0.3	5.8 ± 0.3	5.8 ± 0.4	5.8 ± 0.4	5.7 ± 0.5	5.8 ± 0.3

* Significantly different from C-Run at $p < 0.05$.
** Significantly different from C-Run at $p < 0.01$.
\# Significantly different from T-Run$_{5\%}$ at $p < 0.05$.
\#\# Significantly different from T-Run$_{5\%}$ at $p < 0.01$.
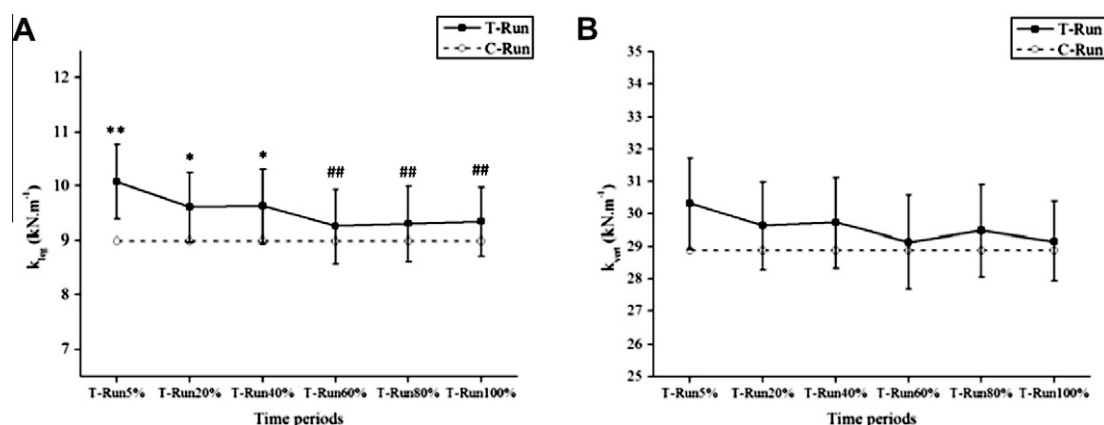
Fig. 2. Changes in k_{leg} (A) and k_{vert} (B) during T-Run. The dash lines represent the mean value measured during C-Run. Significantly different from C-Run at *$p < 0.05$; **$p < 0.01$. Significantly different from T-Run$_{5\%}$ at #$p < 0.05$; ##$p < 0.01$.

3.2.2. Time course during T-Run

t_c increased significantly after T-Run$_{40\%}$ (+3.2% than T-Run$_{5\%}$ at T-Run$_{100\%}$, $p = 0.02$) but t_f decrease during T-Run was not significant. A significant decrease of k_{leg} was observed after T-Run$_{60\%}$ (10.08 ± 1.94 vs. 9.34 ± 1.77 kN m^{-1}, for T-Run$_{5\%}$ and T-Run$_{100\%}$, respectively, $p = 0.03$). Concomitant significant F_{max} decrease (−4.0% than T-Run$_{5\%}$ at T-Run$_{100\%}$, $p = 0.02$) and significant ΔL increase (+4.9% than T-Run$_{5\%}$ at T-Run$_{100\%}$, $p = 0.03$) were observed, after T-Run$_{80\%}$ and at T-Run$_{100\%}$, respectively.

3.2.3. C-Run vs. T-Run$_{100\%}$

At T-Run$_{100\%}$, k_{leg} was not significantly different from its C-Run value (8.99 ± 1.75 vs. 9.34 ± 1.77 kN m^{-1}, for C-Run and T-Run$_{100\%}$, respectively, $p = 0.18$). Similarly, all SMM parameters were not significantly different from their value measured during C-Run.

3.3. EMG parameters

The mean curves of the EMG RMS linear envelopes during C-Run, the initial phase of the triathlon run (T-Run$_{5\%}$) and at its end (T-Run$_{100\%}$) are presented in Fig. 3. The time course of the mean EMG RMS values during C-Run and T-Run are presented in Table 3.

3.3.1. C-Run vs. T-Run$_{5\%}$

EMG activity increased significantly for VM ($p = 0.01$) and RF ($p = 0.01$) during the pre-contact phase, but no significant change was observed for these muscles during the other periods of the stride. We observed no significant changes in EMG RMS values

for the seven other muscles, when considering braking phase, propulsive phase, flight phase, and pre-contact phase ($p > 0.05$).

3.3.2. Time course during T-Run

EMG activity decreased for VM ($p < 0.04$), VL ($p < 0.04$), RF ($p < 0.005$) and SOL ($p = 0.04$, when comparing T-Run$_{5\%}$ and T-Run$_{100\%}$ values) during the pre-contact phase after T-Run$_{40\%}$ and for SOL and GaM during braking phase until T-Run$_{80\%}$ ($p < 0.05$).

3.3.3. C-Run vs. T-Run$_{100\%}$

Lower EMG activity was observed only for GaM during braking phase (−16%, $p = 0.03$). The eight other muscles demonstrated no significant difference during the four periods of the stride.

3.4. Physiological parameters

$\dot{V}O_2$, HR and [La$^-$]$_b$ reached 91.1 ± 6.6% $\dot{V}O_2$max, 93.0 ± 5.8% HR$_{max}$ and 7.8 ± 0.7 mmol L^{-1} at T-Run$_{100\%}$, respectively. All these variables were higher at T-Run$_{100\%}$ than their respective reference value (C-Run). The subjects considered exercise more than "very difficult" at T-Run$_{100\%}$ (17.5 ± 0.5 on Borg scale).

4. Discussion

The purpose of the present study was to describe the behavior of the spring–mass model during a run to exhaustion performed after a cycle exercise by trained triathletes. We also investigated if associated EMG activities in nine lower limb muscles would explain potential mechanical changes. The most important finding
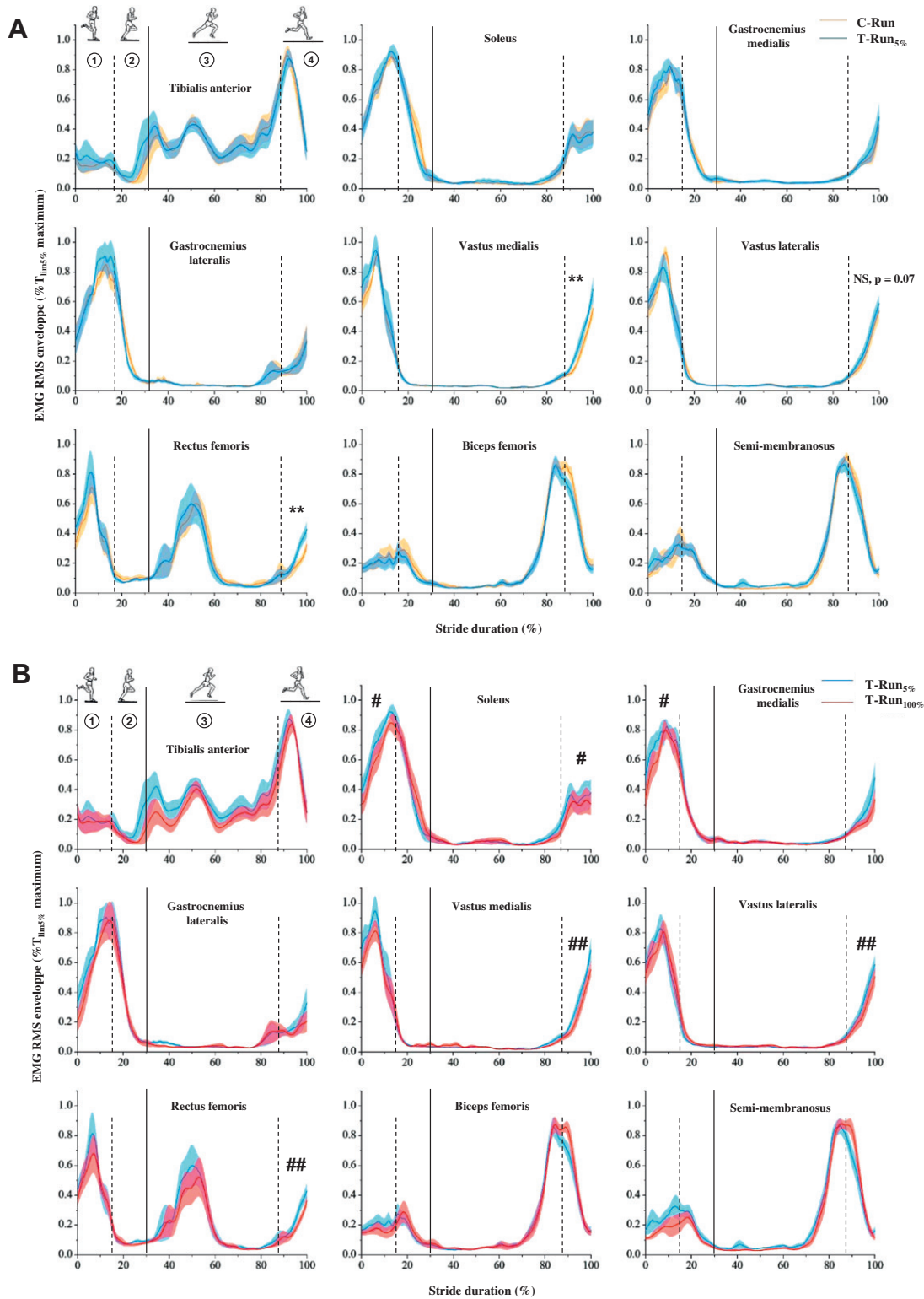
Fig. 3. Ensemble curves of EMG RMS linear envelope for nine lower limb muscles obtained during the control-run (C-Run, black lines), at the start (gray lines) and at the end (dashed lines) of the run to exhaustion of the cycle-to-run combination (T-Run). Each profile represents the mean obtained from averaging individual data across 30 consecutive strides, normalizing to the mean RMS calculated during the complete stride of C-Run ("reference pattern"), and further averaging across the 10 triathletes. Dashed vertical lines represent the end of the contact phase; (1) pre-contact phase (100 ms before ground contact); (2) braking phase (first half of the ground contact); (3) propulsive phase (second half of the ground contact), and (4) flight phase (excluding the pre-contact phase). BF, *biceps femoris*; GL, *gastrocnemius lateralis*; GM, *gastrocnemius medialis*; RF, *rectus femoris*; SM, *semimembranosus*; SOL, *soleus*; TA, *tibialis anterior*; VL, *vastus lateralis*; VM, *vastus medialis*. Significantly different from C-Run at $^{*}p < 0.05$; $^{**}p < 0.01$. Significantly different from T-Run$_{5\%}$ at $^{\#}p < 0.05$; $^{\#\#}\,p < 0.01$.

was that k_{leg} increased transiently at the beginning of the run, before decreasing along the run to exhaustion. We did not report any statistical difference in k_{leg} value at the end of T-Run with its baseline value, recorded in a non fatigued state. This spring–mass behavior was consistent with EMG activity modifications. EMG RMS values of both ankle and knee extensors during the

Table 3
Values (Mean ± SE, mV) of EMG-RMS of the nine lower limb muscles during pre-activation and braking phases in the control (C-Run) and the exhaustive run (T-Run). TA: *tibialis anterior*, SOL: *soleus*, GaL: *gastrocnemius lateralis*, GaM: *gastrocnemius medialis*, VL: *vastus lateralis*, VM: *vastus medialis*, RF: *rectus femoris*, SM: *semimembranosus*, BF: *biceps femoris*. TA: *tibialis anterior*, SOL: *soleus*, GaL: *gastrocnemius lateralis*, GaM: *gastrocnemius medialis*, VL: *vastus lateralis*, VM: *vastus medialis*, RF: *rectus femoris*, SM: *semimembranosus*, BF: *biceps femoris*.

Phase	Muscles	C-Run	T-Run$_{5\%}$	T-Run$_{20\%}$	T-Run$_{40\%}$	T-Run$_{60\%}$	T-Run$_{80\%}$	T-Run$_{100\%}$
Pre-activation	TA	244 ± 41	228 ± 32	214 ± 28	206 ± 35	205 ± 35	206 ± 37	209 ± 34
	SOL	71 ± 14	81 ± 19	75 ± 16	71 ± 16	67 ± 14	62 ± 10	59 ± 8[#]
	GaM	110 ± 26	108 ± 27	103 ± 23	107 ± 24	99 ± 23	94 ± 21	92 ± 20[*]
	GaL	63 ± 22	58 ± 16	55 ± 13	50 ± 11	49 ± 13	51 ± 12	51 ± 11
	VM	100 ± 15	121 ± 17[*]	107 ± 14	112 ± 18	104 ± 16[#]	103 ± 16[##]	97 ± 15[##]
	VL	113 ± 20	125 ± 20	101 ± 15	106 ± 18	96 ± 17	95 ± 17[#]	92 ± 17[##]
	RF	28 ± 8	34 ± 8[**]	31 ± 7	29 ± 7	27 ± 6[##]	27 ± 6[##]	27 ± 6[##]
	BF	183 ± 25	166 ± 24	180 ± 25	191 ± 25	196 ± 26[#]	200 ± 25[#]	194 ± 23
	SM	181 ± 26	158 ± 25	170 ± 28	178 ± 28	175 ± 25	178 ± 27	177 ± 27
Braking phase	TA	64 ± 14	66 ± 11	68 ± 11	67 ± 10	61 ± 8	61 ± 7	60 ± 8
	SOL	257 ± 28	277 ± 34	260 ± 30	274 ± 30	262 ± 25	246 ± 25[#]	241 ± 25[#]
	GaM	273 ± 18	281 ± 24	259 ± 16	267 ± 22	254 ± 20	246 ± 15[#]	241 ± 9[*,#]
	GaL	225 ± 23	239 ± 32	231 ± 39	235 ± 37	221 ± 35	222 ± 33	216 ± 33
	VM	241 ± 25	252 ± 26	226 ± 24	237 ± 25	230 ± 22	232 ± 26	228 ± 24
	VL	240 ± 45	230 ± 38	219 ± 25	227 ± 21	226 ± 18	220 ± 15	232 ± 20
	RF	77 ± 16	86 ± 17	83 ± 17	77 ± 16	76 ± 16	76 ± 14	79 ± 16
	BF	81 ± 20	83 ± 12	67 ± 11	59 ± 11	60 ± 12	51 ± 11	59 ± 12
	SM	70 ± 15	66 ± 15	59 ± 13	55 ± 11	55 ± 10	50 ± 9	53 ± 11

[*] Significantly different from C-Run value at $p < 0.05$.
[**] Significantly different from C-Run value at $p < 0.01$.
[#] Significantly different from T-Run$_{5\%}$ at $p < 0.05$.
[##] Significantly different from T-Run$_{5\%}$ at $p < 0.01$.

pre-contact phase and/or the braking phase decreased along time after an increase of knee extensors activity during the pre-contact phase at the beginning of the run to exhaustion.

4.1. Spring–mass behavior

The first and most noticeable finding of the present study was that k_{leg} increased at the beginning of T-Run, after completion of the cycling exercise. All of the 10 triathletes demonstrated the same k_{leg} time-course changes although a high inter-individual variability is usually reported for this parameter (Dutto and Smith, 2002; Hunter and Smith, 2007; Rabita et al., 2011). The increase of k_{leg} at T-Run$_{5\%}$ was unexpected, when considering that previous studies investigating the SMM behavior during exhaustive runs performed under $\dot{V}O_{2max}$ have always reported maintenance or decrease of k_{leg} with time (Dutto and Smith, 2002; Girard et al., 2010; Hunter and Smith, 2007; Morin et al., 2011; Rabita et al., 2011; Slawinski et al., 2008). This finding highlighted that the cycle-to-run transition represented a particular context for k_{leg} time course. The main hypothesis would consider that this transitional stiffness adaptation might be related both to the temporary kinematic modifications induced by the transition between cycling and running and to the pacing strategy typically employed by triathletes during the cycle-to-run transition. On the one hand, Hausswirth et al. (1997) showed that triathletes adopted a more forward leaning posture particularly during the initial phase of a simulated triathlon (30 min swimming, 60 min cycling, 45 min treadmill running), when compared to an isolated run performed at the same speed. This change in posture would have implied a forward position of the center of mass at the foot contact and, then, a reduced angle swept by the leg-spring during this ground contact phase which could have explained a lower ΔL between C-Run and T-Run$_{5\%}$. At the same time, we suggest that subjects of the present study may have mimicked the systematic spontaneous fast start strategy reported by triathlon field-based studies (Le Meur et al., 2009, 2011), and that may have induced higher pre-activation of their knee extensors and higher F_{max} at T-Run$_{5\%}$. Because running speed was externally imposed by the treadmill, we hypothesized that the present protocol would have artificially prevented triathletes from

extending this strategy during the contact phase. Further investigations are required to test this hypothesis and to determine whether this transient adaptation is beneficial or not.

The second main finding of this study was that k_{leg} decreased during the triathlon run, when compared with its value at T-Run$_{5\%}$. This finding was in accordance with aforementioned studies (Dutto and Smith, 2002; Rabita et al., 2011) and research on sprint running (Hobara et al., 2010; Morin et al., 2006) in which this parameter was reported to decrease with time. Using a force platform system, Rabita et al. (2011) showed that k_{leg} decrease during a run to exhaustion at 95% v $\dot{V}O_{2max}$ was positively related with modifications of flight time and negatively with contact time. In the same time, a decrease of peak vertical force was observed. The latter was related with the decrease of the angle velocity vector at toe off. Considering that a decrease of flight time and an increase of contact time were observed during T-Run, a similar modification of stride mechanical parameters may have explained the reported decrease of k_{leg} in the present study.

Regarding k_{vert}, no change was observed for the duration of the protocol. This result differs from most aforementioned studies (Dutto and Smith, 2002; Girard et al., 2010; Hobara et al., 2010; Morin et al., 2006), where this parameter was reported to decrease during free-paced exercise. Nevertheless, the subjects demonstrated a positive pacing strategy in these protocols, whereby after a peak running speed was reached, they progressively slowed down, making it difficult to interpret these results because k_{vert} is positively influenced by running speed (Arampatzis et al., 1999). Interestingly, the maintenance of k_{vert} value throughout the present protocol was in line with the results from Rabita et al. (2011), which were collected with a force platform system. These authors reported no significant change of k_{vert} during an isolated time-to-exhaustion running test performed to exhaustion (∼10 min) by elite triathletes; the subjects compensated the fatigue-induced impairment of the neuromuscular function of force production by flattening the trajectory of their center of mass. All together, these results demonstrated that trained triathletes are able to keep k_{vert} constant during a running time to exhaustion by maintaining the vertical displacements of their center of mass despite the onset of fatigue.

4.2. Electromyographic activity

k_{leg} increase at T-Run$_{5\%}$ was consistent with higher EMG activity during the pre-contact phase for VM and RF. Despite no significant difference ($p = 0.07$), the tendency of VL to increase has to be pointed out, considering that its RMS values increased in nine of the ten triathletes studied. This finding was consistent with the decrease of contact time immediately after the cycle exercise, and suggested that triathletes reduced knee flexion during the braking phase. Higher activation of motor units in knee extensors muscles is likely to have increased the capacity of triathletes to resist the stretch-load by increasing knee stiffness during the braking phase of the stride. This interpretation is in agreement with earlier studies focusing on hopping, which noted that k_{leg} partly depends on pre-activation during the aerial phase (Dyhre-Poulsen et al., 1991; Gollhofer and Kyrolainen, 1991). Centrally programmed neuromuscular activity prior to the contact may be seen as the decisive mechanism in the regulation of the stiffness behavior of the lower limb during running.

Similarly, k_{leg} decrease along T-Run was consistent with the concomitant reduction of the EMG RMS during the pre-contact phase for VM, VL, RF, and SOL from T-Run$_{60\%}$, and during the braking phase for SOL and GaM at T-Run$_{80\%}$. To the best of our knowledge, this study is the first to describe the time course of the EMG RMS in nine leg muscles during a submaximal run performed until exhaustion, considering that the large majority of past studies investigated the influence of fatigue on muscular recruitment during running using a pre- and post-exercise design protocol (Avela and Komi, 1998; Hausswirth et al., 2000; Nummela et al., 2008). Nummela et al. (2008) reported similar results by well-trained runners during a maximal 20 m run performed before and immediately after a self-paced 5 km run. Their results revealed (i) a decreased of the EMG activity for both the VM and the GaL during the pre-contact phase; and, (ii) a significant correlation between the decreased pre-activation and increased contact times. Similar findings were also observed after a 10 km time trial (Paavolainen et al., 1999). A decreased pre-activation and a significant relationship between the decreased pre-activation and decrease of horizontal ground reaction force in the braking phase were reported in well-trained runners. In the same way, Avela and Komi (1998) observed a reduced EMG activity in SOL and VM during a series of 10 maximal drop jumps performed on a sledge ergometer before and after a marathon run (42.2 km). Interestingly, analysis of the SMM behavior during the exhaustive run revealed that k_{leg} decrease was explained by the increase of contact times (+3.8% between T-Run$_{5\%}$ and T-Run$_{100\%}$).We suggested that the progressive decrease of muscle activity during the pre-contact phase (VM, VL, RF, SOL) and the braking phase (GaM, SOL) is likely to have partly explained these results. Given the mechanical function of these muscles during pre-contact and braking phases of the stride (Kyrolainen et al., 2005), we hypothesized that a decrease of their EMG activity during these phases may have induced an increase of ankle and knee flexions during the ground contact (i.e. higher ΔL values). These adaptations may explain the progressive decrease of k_{leg} reported during T-Run. Further investigations analyzing joints angles during the triathlon run are required to confirm this hypothesis.

The concomitant decrease of k_{leg} and changes of muscular activity reported during T-Run could be a result of: (1) neuromuscular impairments occurring with fatigue during running; (2) a progressive alleviation of prior cycling effect; or, (3) both situations. Lepers et al. (2001) showed a significant decrease in maximal twitch tension (i.e., alteration of the contractile properties) of the quadriceps group in well-trained triathletes after 30 min of cycling at 80% of the maximal aerobic power. Despite cycling intensity was a little lower in the present study ($\sim$72% of the maximal aerobic power),

triathletes were engaged in a subsequent run until exhaustion immediately after cycling, making the neuromuscular fatigue hypothesis during T-Run credible. Both physiological and perceptual parameters indicated indeed that the cycle-to-run combination was highly demanding. The triathletes attained 93% HR$_{max}$, 91% $\dot{V}O_{2max}$, a [La$^-$]$_b$ value of 7.8 mmol L^{-1} at the end of the run, and considered the exercise more than "very difficult" (17.5 on Borg scale). On the other hand, the absence of significant difference between the control run and the end of the triathlon run in stride amplitude, k_{leg} and EMG activity in eight of the nine muscles investigated suggested that the decrease of these parameters during T-Run may have been related to the progressive alleviation of the prior cycling effect during the subsequent run. In addition, most of muscle activity changes occurred during the pre-contact phase, suggesting that these EMG adaptations were mainly related to the modifications of the central command. During the contact phase, EMG activity decreased for GaM and SOL, but both F_{max} and ΔL remained unchanged, when compared with their C-Run level after T-Run$_{5\%}$. Without excluding the possibility of potential neuromuscular deteriorations, it showed that the capacities of the neuromuscular system to produce force and to resist the stretch-load were preserved at the end of the run to exhaustion. On the basis of these results, we can reasonably hypothesize that the concomitant EMG and biomechanical modifications observed during T-Run were at least partially associated with a progressive alleviation of cycling effect on the neural command during the subsequent run. Further investigations using direct neuromuscular fatigue measurements are needed to better separate the influence of muscle fatigue (i.e., alteration of contractile properties) from transitional adjustments after cycling.

4.3. Limitations

One of the main limitations of the present study was that it cannot be ruled out that the assumptions underlying the computation method proposed by Morin et al. (2005) may not be questioned when fatigue occurs. Nevertheless, the changes in k_{leg} and k_{vert} reported in the literature for comparable exercises, in terms of duration and running speed, have always been homogeneous, whatever the methodology employed (i.e., force plate measurements or model). For instance, the spring–mass behavior due to the fatigue induced by an ultra-marathon race using the computation method (Morin et al., 2011) was in accordance with the results observed during a 24 h run race using a force plate system (Morin et al., 2010). A similar observation can be made by comparing the results of Girard et al. (2011) and Hobara et al. (2010) in sprint running. These findings lead us to think that using Morin's model (2005) during a run performed until exhaustion does not seem inconsistent. However, specific investigations have to be undertaken to quantify specifically this issue.

Furthermore, the present results could have been influenced by the fact that EMG was only recorded on the right leg while spring mass parameters were averaged from the two legs. Indeed, asymmetries between right and left legs have been previously reported in running (Dalleau et al., 1998). Considering the number of tested muscles in the present study ($n = 9$), it was impossible for us to record both lower limbs. Obviously, we cannot exclude that our subjects did not present such dissymmetry. However, the consistency between the evolution of the spring–mass behavior and EMG changes suggests that such influence was moderate. New data are necessary to definitively stipulate on this subject.

In conclusion, the present study demonstrated that the time course of leg stiffness was consistent with EMG activity changes during a $\sim$45 min cycle-to-run combination to exhaustion by trained triathletes. A transient increase of leg stiffness associated with a transitional higher activity of knee extensors during the pre-contact phase was reported during the initial phase of the triath-

lon run. Then, leg stiffness decreased, and returned to its baseline level, while EMG activity of both ankle and knee extensors revealed a similar time course. Without excluding the possibility of potential neuromuscular alterations, the capacities of the neuromuscular system to produce force and to resist the stretch-load were preserved at the end of the cycle-run exercise to exhaustion.

Acknowledgments

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