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Spring–Mass Behavior during Exhaustive Run at Constant Velocity in Elite Triathletes

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ABSTRACT

RABITA, G., J. SLAWINSKI, O. GIRARD, F. BIGNET, and C. HAUSSWIRTH. Spring – Mass Behavior during Exhaustive Run at Constant Velocity in Elite Triathletes. *Med. Sci. Sports Exerc.*, Vol. 43, No. 4, pp. 685 – 692, 2011. **Purpose:** The aims of this study were i) to evaluate changes in leg-spring behavior during an exhaustive run in elite triathletes and ii) to determine whether these modifications were related to an increase in the energy cost of running (C_r). **Methods:** Nine elite triathletes ran to exhaustion on an indoor track at a constant velocity corresponding to 95% of the velocity associated with the maximal oxygen uptake (mean T SD = 5.1 T 0.3 m/s¹, time to exhaustion = 10.7 T 2.6 min). Vertical and horizontal ground reaction forces were measured every lap (200 m) by a 5-m-long force platform system. C_r was measured from pulmonary gas exchange using a breath-by-breath portable gas analyzer. **Results:** Leg stiffness (\downarrow 13.1%, $P < 0.05$) and peak vertical (\downarrow 9.2%, $P < 0.05$) and propulsive (\downarrow 7.5%, $P < 0.001$) forces decreased significantly with fatigue, whereas vertical stiffness did not change significantly. Leg and vertical stiffness changes were positively related with modifications of aerial time ($R^2 = 0.66$, $P < 0.01$ and $R^2 = 0.72$, $P < 0.01$, respectively) and negatively with contact time ($R^2 = 0.71$, $P < 0.01$ and $R^2 = 0.74$, $P < 0.01$, respectively). Alterations of vertical forces were related with the decrease of the angle of velocity vector at toe off ($R^2 = 0.73$, $P < 0.01$). When considering mean values of oxygen uptake, no change was observed from 33% to 100% of the time to exhaustion. However, between one-third and two-thirds of the fatiguing run, negative correlations were observed between oxygen consumption and leg stiffness ($R^2 = 0.83$, $P < 0.001$) or vertical stiffness ($R^2 = 0.50$, $P < 0.03$). **Conclusions:** During a constant run to exhaustion, the fatigue induces a stiffness adaptation that modifies the stride mechanical parameters and especially decreases the maximal vertical force. This response to fatigue involves greater energy consumption. **Key Words:** MUSCULOSKELETAL STIFFNESS, RUNNING, FATIGUE, ENERGY COST, TRIATHLON

Many studies have attempted to identify factors involved in performance of elite triathletes by analyzing biomechanical parameters with exercise duration during triathlon (3,18). Although swimming and cycling have both energetic (11,26) and mechanical (9,12) influences on the subsequent mode(s) of locomotion, triathlon overall finishing position is strongly determined by running performance (38). Consequently, a better understanding of the effects of running fatigue as it influences mechanical modification and metabolic energy costs in triathletes continues to be a challenge to improve training programs.

In humans, many studies have been carried out to characterize running using the spring – mass model (SMM) (4,6,27). This model consists of a point mass bouncing on

a massless spring. SMM provides a well-accepted theoretical basis from which leg stiffness (k_{leg} , ratio of the vertical ground reaction force to the leg-spring compression at middle of the stance phase) and vertical stiffness (k_{vert} , ratio of the maximal force to the vertical downward maximal displacement of the center of mass (COM)) can be determined. These types of mechanical stiffness have been frequently used for characterization of running mechanics because they influence the regulation of temporal and kinematic variables (14,30).

Numerous studies specifically analyzed the changes in biomechanical parameters during running in fatigue conditions (2,7,25,35), although only few explored the evolution of leg stiffness and its relationships with step temporal variables. Furthermore, the results have been quite contradictory. For constant and moderate running intensities (under the lactic threshold), Dutto and Smith (13) showed that k_{leg} and k_{vert} both decreased with fatigue, whereas Hunter and Smith (22) reported no significant change. Both studies, however, reported that stride frequency was more strongly related to k_{vert} than k_{leg} . For severe running intensities (above the lactic threshold), Slawinski et al. (35) did not detect any variation of k_{leg} or k_{vert} before or after a 2000-m maximal run. In contrast, Girard et al. (16) found a decrease of k_{vert} while k_{leg} remained constant during a self-paced 5000-m run. For sprint running intensities, the

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fatigue-induced changes in mechanical stiffness were concluded to be mainly due to modifications in the COM vertical displacement rather than changes in the maximal force; furthermore, it appeared that k_{vert} was more affected by the fatigue state than k_{leg} (20,29). Nevertheless, neither severe nor sprint studies imposed a constant pace for the run, although temporal, kinematic, and kinetic parameters associated with the spring – mass stiffness had been shown to be directly dependent on the running speed (1,6,27).

To our knowledge, changes in spring – mass behavior on the energy cost of running (C_r) at constant velocity have only been investigated for moderate intensities (19). The authors did not find a clear relationship between energy cost of running and changes in frequency or stiffness. However, other studies showed that k_{leg} and/or k_{vert} are among those biomechanical parameters that exhibit the strongest association to the C_r (7,10,19,23,28,35).

The aims of this study were, therefore, to characterize changes in leg-spring behavior in elite triathletes during a constant velocity exhaustive run and to verify whether these modifications were related to the increase in the energy cost of running. On the basis of consideration of the literature, we hypothesized that i) k_{leg} and k_{vert} would decrease during the run, and ii) these decreases would be inversely related with the changes in maximal oxygen uptake.

METHODS

Subjects

Nine elite triathletes belonging to the French National Team, including six men (mean T SD: age = 23.2 T 3.2 yr, height = 181.7 T 2.4 cm, weight = 68.3 T 5.4 kg) and three women (age = 25.0 T 4.4 yr, height = 166.7 T 4.2 cm, weight = 58.3 T 3.2 kg), were recruited to participate in the study. All of these athletes had competed at international level during the year. Throughout this year, the range of training distances per week was approximately 20 – 25 km in swimming, 200 – 350 km in cycling, and 55 – 75 km in running. Procedures were explained to each subject before participation. Written informed consent was obtained from each of the subjects, and the study was conducted according to the Declaration of Helsinki. This study was approved by the local ethics committee before its initiation.

Procedures

Two runs on an indoor 200-m synthetic track were required of each subject. The first run was carried out as a graded exercise test (3-min stages) to determine maximal oxygen uptake ($\dot{V}O_{2\text{max}}$) and its associated velocity ($v\dot{V}O_{2\text{max}}$). The second run, performed 2 d later, was a constant velocity run performed until exhaustion at a speed corresponding to 95% of $v\dot{V}O_{2\text{max}}$. Throughout the tests, the subjects adopted the required velocity by using an audio rhythm that gave the time allotted to cover 20 m; visual marks had been set at 20-m intervals along the track.

Data Collection

Ground reaction force. Once per lap during the constant run to exhaustion, the vertical and horizontal components of the ground reaction forces were measured by a 5-m-long force platform system (natural frequency Q 500 Hz). The system consisted of five individual force plates (1.00 × 1.00 m) connected in series, covered with a tartan mat, and leveled with the stadium track. It allowed recording ground reaction force of two or three steps per lap (according to the step length and the separated distance of the first foot contact from the entrance of the force plate area). Each force platform was equipped with Kistler piezoelectric sensors (KI 9067; Kistler, Wintertur, Switzerland). The force signals were sampled at 500 Hz.

$\dot{V}O_2$ response. Values of oxygen uptake were determined breath by breath during both the incremental test and the constant run to exhaustion (Cosmed K4b², Rome, Italy). Gas analyzer was calibrated before each test using ambient air ($O_2 = 20.93\%$ and $CO_2 = 0.03\%$) and a gas mixture of known composition ($O_2 = 16.0\%$ and $CO_2 = 5.0\%$). 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, bidirectional digital turbine (28-mm diameter). This turbine was calibrated before each test with a 3-L syringe (Hans Rudolph Inc., Dallas, TX).

Data Analyses

Spatiotemporal parameters. A typical example of changes in vertical (F_z) and horizontal (F_y) components of ground reaction force are presented in Figure 1. Contact and aerial phases (i.e., contact time, t_c (s), and aerial time, t_a (s)) were defined when the vertical force was more than and less than 50 N, respectively. Active peak amplitude of vertical force ($F_{z\text{max}}$), peak braking ($F_{y\text{min}}$) and push-off ($F_{y\text{max}}$) forces, step frequency ($f = (t_a + t_c)^{-1}$, in hertz), and step length ($SL = V_{\text{forward}} \cdot f^{-1}$, in meters) were also determined. Anteroposterior forces were used to determine

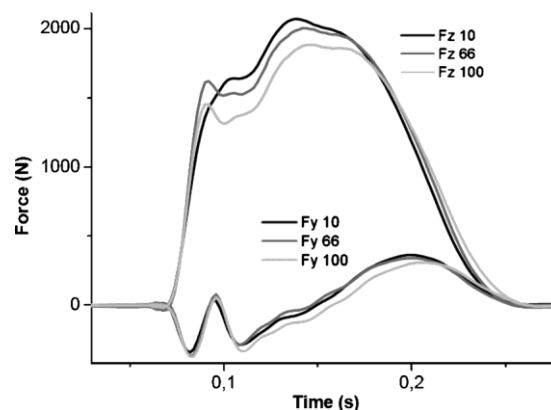


FIGURE 1—Typical example of changes in vertical (F_z) and horizontal (F_y) reaction force components measured at the beginning (10%), at the second-third (66%), and at the end (100%) of the exhaustive run.

the braking and push-off phases during ground contact when the anteroposterior force was negative and positive, respectively. Braking and push-off impulse (B_{imp} and P_{imp} , respectively) values were determined from the product of the effective force applied to the running surface and foot-ground contact times of these respective phases. Force data were then used for calculating leg-spring behavior parameters.

SMM characteristics. Leg and vertical stiffness during

running was calculated using a classical method (14,27). Leg stiffness (k_{leg} , $kNIm^{-1}$) was defined as follows:

$$k_{leg} \approx F_{zmax} / \Delta L \quad (1)$$

where F_{zmax} was the maximal vertical ground reaction force and ΔL was the leg compression at the middle of the stance phase, that is, when F was maximal and the leg was maximally compressed. ΔL was calculated from the maximal vertical displacement of the COM, Δy , the initial length of the leg spring, L_0 (vertical distance from the ground to the greater trochanter during standing), and half of the angle swept by the leg spring during the contact phase, θ :

$$\Delta L \approx \Delta y + L_0(1 - \cos \theta) \quad (2)$$

The vertical displacement Δy was calculated by integrating the vertical acceleration twice (constants of integration were calculated according to the methodology proposed by Cavagna (8)). θ was calculated from the contact time (t_c), the forward speed (u), and the L_0 , according to the following formula:

$$\theta \approx \sin^{-1}(\Delta u / t_c) + 2L_0 / u \quad (3)$$

where Δu represented the horizontal distance traveled by the COM (in meters) during the contact phase.

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

$$k_{vert} \approx F_{zmax} / \Delta y \quad (4)$$

The angle (θ , in degrees) of the velocity vector of the COM at toe off was calculated as:

$$\tan \theta \approx V_z / V_x \quad (5)$$

where V_z and V_x represented the vertical and the horizontal velocities of the COM at toe off. Both were calculated using integration against time of the vertical and horizontal acceleration of the COM (8).

For every parameter, the average of two laps (i.e., four to six steps) around one-tenth, one-third, and two-thirds of the time to exhaustion were calculated and averaged. The values corresponding to the end of the run were calculated from the data of the two last laps. Then, the measures were effectively recorded at 9.4% T 0.8%, 33.4% T 1.0%, 66.1% T 1.1%, and 95.3% T 0.9% of the time to exhaustion. To simplify, these times were noted 10%, 33%, 67%, and 100%. The values were normalized with respect to those obtained at the beginning (one-tenth) of the run to exhaustion.

Energy cost of running. The breath-by-breath $\dot{V}O_2$ data were fitted to a single-exponential function (36).

According to Gaesser and Poole (15), a first steady state of oxygen uptake could be reached after 3 min of exercise during a constant velocity run performed at a severe intensity. Thus, $\dot{V}O_2$ changes were normalized with respect to the values obtained at 33% of the time to exhaustion. Then, the C_r ($J/kg^{1/2}Im^{-1}$) was calculated as

$$C_r \approx \dot{V}O_2 E_{O_2} V_{95}^{-1} \quad (6)$$

where $\dot{V}O_2$ was the oxygen uptake ($mL O_2/Im^{-1}$), E_{O_2} ($21.3 J/mL O_2^{-1}$) was the energy equivalent of 1 mL O_2 for a respiratory exchange ratio of 1, V_{95} was the velocity (mIm^{-1}) during the run to exhaustion, and M was the body mass (kg).

Statistical Analysis

For all tested parameters, the effect of fatigue was determined by a single factor ANOVA for repeated measures (33%, 66%, and 100% of the time to exhaustion). When a significant main effect was observed, the *post hoc* Sheffé test was performed. Pearson's correlation coefficients were used to examine the relationships between leg-spring stiffness

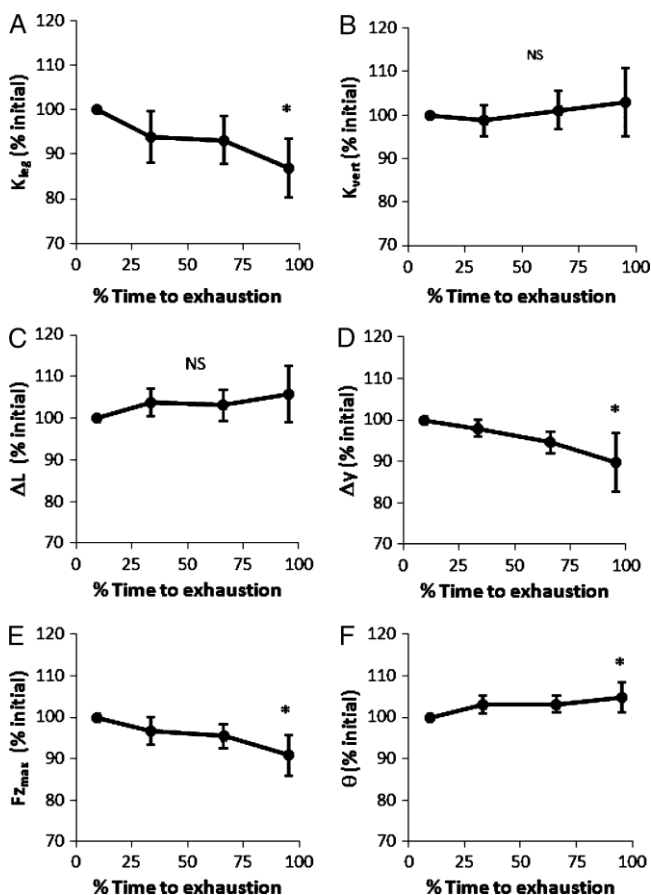


FIGURE 2—Evolution of the mean normalized values (± SD) in (A) leg stiffness (k_{leg}), (B) vertical stiffness (k_{vert}), (C) leg compression (ΔL), (D) vertical displacement of the COM (Δy), (E) vertical component of reaction force (F_{zmax}), and (F) angle of the spring leg at touchdown (θ). Data were normalized and expressed as the percentage of the values obtained at 10% of the time to exhaustion. *Significant difference at $P < 0.05$.

(k_{leg} and k_{vert}), C_r , and spatiotemporal parameters. Values have been presented as mean T SD. All statistical analyzes were conducted at $P < 0.05$.

RESULTS

During the incremental test, $\dot{V}O_{2\max}$ and $v\dot{V}O_{2\max}$ mean values were equal to 71.5 T 6.5 mLkg⁻¹Imin⁻¹ and 5.1 T 0.3) mLs⁻¹, respectively. During the second test, the mean time to exhaustion was 10.7 T 2.6 min, which corresponded to a mean distance of 3258 T 819 m or 16.3 T 4.1 laps. During the interval 33% – 100% of the time to exhaustion, $\dot{V}O_2$ values, from 65.1 T 3.9 to 63.6 T 4.1 mLkg⁻¹Imin⁻¹, did not change significantly ($P > 0.05$).

Leg stiffness decreased by 13.1% with exhaustion ($P = 0.01$; Fig. 2A). The maximal vertical force during contact (F_{zmax}) decreased significantly with fatigue (j9.2%; Fig. 2E), whereas the change in leg-spring compression ($\$L$) was not significant (Fig. 2C). The vertical stiffness did not show any significant change ($P > 0.05$; Fig. 2B). Indeed, $\$y$ decreased proportionally with F_{zmax} (Fig. 2D). All absolute mean values are presented in Table 1.

The normalized changes and raw mean values of the temporal and kinematic parameters are presented in Table 1. A slight but significant increase in the step frequency ($P < 0.05$) was observed despite a significant increase in the contact time (+4.3%, $P < 0.05$). This result was explained by a greater decrease in the aerial time. The step length decreased significantly ($P < 0.05$). The horizontal distance traveled by the COM during the contact phases increased. Braking and propulsive impulse did not change significantly ($P > 0.05$). Contrary to the normalized values of F_{ymin} (i.e., the maximal braking anteroposterior force), a significant decrease was observed for F_{ymax} ($P < 0.001$; Table 1). The angle of the velocity vector at takeoff significantly decreased (j18.3%).

The relationships between k_{leg} , k_{vert} , and F_{zmax} versus selected temporal, kinematic, and dynamic parameters are presented in Table 2, whereas the significant relationships have been included in Figures 3A – E. The relationships between normalized changes in horizontal impulses were found to be significantly related with $\$$ ($R = 0.54$, $P = 0.021$ for B_{imp} and $R = 0.53$, $P = 0.022$ for P_{imp}) but not with minimal or maximal F_{ymin} or F_{ymax} changes.

TABLE 1. Evolution of spatiotemporal and horizontal dynamic parameters.

| | 10% | 33% | 67% | 100% | P |
|---|---------------|---------------|----------------|-------------------|-------|
| Normalized data (%) | | | | | |
| Normalized spatiotemporal parameters | | | | | |
| t_c | – | 102.6 (3.9) | 102.8 (3.7) | 104.3 (6.3)* | 0.031 |
| t_a | – | 97.6 (5.7) | 94.5 (6.3)* | 92.1 (7.7)**† | 0.010 |
| f_{step} | – | 99.6 (1.9) | 101.0 (2.4) | 101.3 (2.2)*† | 0.048 |
| L_{step} | – | 99.4 (1.6) | 99.1 (1.2) | 97.7 (1.8)**† | 0.001 |
| > | – | 93.3 (12.1) | 88.9 (8.9)* | 81.7 (11.2)****† | 0.001 |
| Normalized horizontal dynamic parameters | | | | | |
| F_{ymin} | – | 99.8 (11.3) | 97.0 (9.2) | 97.1 (8.0) | ns |
| B_{imp} | – | 102.6 (4.8) | 100.0 (4.6) | 98.9 (4.1) | ns |
| F_{ymax} | – | 97.6 (4.0) | 94.3 (4.2)** | 92.5 (2.1)***†† | 0.001 |
| P_{imp} | – | 102.1 (4.8) | 99.5 (4.6) | 98.6 (5.0) | ns |
| Normalized energy parameters | | | | | |
| $\dot{V}O_2$ | – | – | 100.5 (4.2) | 97.7 (4.4) | ns |
| C_r | – | – | 100.5 (4.2) | 97.7 (4.4) | ns |
| Raw data | | | | | |
| Stiffness parameters | | | | | |
| k_{leg} (kNIm ⁻¹) | 11.7 (1.9) | 10.9 (1.3) | 10.8 (1.2) | 10.4 (1.0)* | 0.012 |
| k_{vert} (kNIm ⁻¹) | 44.4 (7.2) | 43.6 (6.3) | 44.5 (5.2) | 45.0 (5.3) | ns |
| F_{zmax} (N) | 1963 (262) | 1893 (235) | 1864 (192) | 1772 (219)* | 0.018 |
| $\$L$ (m) | 0.168 (0.016) | 0.174 (0.010) | 0.173 (0.010) | 0.175 (0.015) | ns |
| $\$y$ (m) | 0.045 (0.004) | 0.044 (0.003) | 0.042 (0.002) | 0.040 (0.006)* | 0.025 |
| $\$$ (deg) | 29.8 (1.3) | 30.6 (0.8) | 30.7 (1.0) | 31.2 (1.3)* | 0.031 |
| Spatiotemporal parameters | | | | | |
| t_c (s) | 0.182 (0.009) | 0.187 (0.006) | 0.187 (0.007) | 0.190 (0.007)* | 0.031 |
| t_a (s) | 0.144 (0.013) | 0.140 (0.013) | 0.135 (0.011)* | 0.132 (0.010)**† | 0.010 |
| f_{step} (Hz) | 3.07 (0.11) | 3.06 (0.09) | 3.10 (0.07) | 3.11 (0.05)*† | 0.048 |
| L_{step} (m) | 1.65 (0.12) | 1.64 (0.13) | 1.63 (0.13) | 1.61 (0.13)**† | 0.001 |
| > (deg) | 7.0 (0.8) | 6.5 (0.8) | 6.2 (0.6)* | 5.7 (0.8)***† | 0.001 |
| Horizontal dynamic parameters | | | | | |
| F_{ymin} (N) | j431 (125) | j432 (139) | j416 (111) | j413 (99) | ns |
| B_{imp} (NIs) | j14.93 (2.09) | j15.37 (2.63) | j14.96 (2.39) | j14.77 (2.10) | ns |
| F_{ymax} (N) | 283.9 (46.6) | 277.5 (47.9) | 267.8 (44.0)** | 261.9 (38.8)***†† | 0.001 |
| P_{imp} (NIs) | 15.05 (2.03) | 15.44 (2.61) | 15.02 (2.38) | 14.85 (2.12) | ns |
| Energy parameters | | | | | |
| $\dot{V}O_2$ (mLkg ⁻¹ Imin ⁻¹) | – | 65.1 (3.9) | 65.4 (4.6) | 63.6 (4.1) | ns |
| C_r (Jkg ⁻¹ Im ⁻¹) | – | 4.57 (0.28) | 4.56 (0.25) | 4.46 (0.33) | ns |

Evolution of spatiotemporal parameters (contact time (t_c), aerial time (t_a), step frequency (f_{step}), step length (L_{step}), and angle of velocity vector at toe off (>)) and horizontal dynamic parameters (minimal horizontal component of the reaction force (F_{ymin}), braking impulse (B_{imp}), maximal horizontal component of the reaction force (F_{ymax}), and propulsive impulse (P_{imp})) at one-third (33%), at two-thirds (67%), and at the end (100%) of the time to exhaustion. Data were normalized and expressed as percent of the values obtained at 10% of the time to exhaustion. ns, not significant.

* $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$, significantly different from the values obtained at 10% of the time to exhaustion.

† $P < 0.05$ and †† $P < 0.01$, significantly different from the values obtained at 33% of the time to exhaustion.

TABLE 2. Correlations between spatiotemporal or horizontal dynamic parameters and stiffness parameters.

| | k_{leg} | | | k_{vert} | | | F_{zmax} | | |
|-------------------------------|-----------|----------------|---------|------------|----------------|---------|------------|----------------|---------|
| | R | R ² | P | R | R ² | P | R | R ² | P |
| Spatiotemporal parameters | | | | | | | | | |
| t_c | j0.84 | 0.71 | 0.003** | j0.86 | 0.74 | 0.001** | j0.079 | 0.01 | ns |
| t_a | 0.81 | 0.66 | 0.005** | 0.85 | 0.72 | 0.001** | j0.135 | 0.02 | ns |
| f_{step} | j0.56 | 0.31 | ns | j0.52 | 0.27 | ns | j0.114 | 0.02 | ns |
| L_{step} | j0.29 | 0.08 | ns | j0.192 | 0.04 | ns | j0.488 | 0.24 | ns |
| > | 0.05 | 0.00 | ns | 0.154 | 0.02 | ns | 0.857 | 0.74 | 0.002** |
| Horizontal dynamic parameters | | | | | | | | | |
| F_{ymin} | j0.03 | 0.00 | ns | 0.07 | 0.01 | ns | j0.08 | 0.01 | ns |
| B_{imp} | j0.55 | 0.30 | ns | j0.46 | 0.21 | ns | j0.43 | 0.18 | ns |
| F_{ymax} | 0.69 | 0.47 | 0.038* | 0.67 | 0.45 | 0.048* | 0.06 | 0.00 | ns |
| P_{imp} | j0.60 | 0.36 | ns | j0.48 | 0.23 | ns | j0.12 | 0.01 | ns |

Correlations between normalized changes (%) of i) spatiotemporal parameters (contact time (t_c), aerial time (t_a), step frequency (f_{step}), step length (L_{step}), and angle of velocity vector at toe off (>)) or ii) horizontal dynamic parameters (minimal horizontal component of the reaction force (F_{ymin}), braking impulse (B_{imp}), maximal horizontal component of the reaction force (F_{ymax}), and propulsive impulse (P_{imp})) and normalized changes (%) of leg stiffness (k_{leg}), vertical stiffness (k_{vert}), and vertical component of reaction force (F_{zmax}). For every parameter, changes were calculated between 10% and 100% of the time to exhaustion. Values significantly related at * $P < 0.05$ and ** $P < 0.01$.

When the results were normalized with respect to the values measured at 33% of the time to exhaustion, no significant correlation was observed between either stiffness or C_r at the end of the constant velocity run (100% of the time to exhaustion). However, between the 33% and 66% interval of the time to exhaustion, normalized changes of both k_{leg} and k_{vert} were found to be correlated with the normalized changes of C_r ($R = j0.91$, $P < 0.001$ and $R = j0.71$, $P < 0.05$, respectively) (Fig. 3D). Normalized changes in both k_{leg} and k_{vert} were not correlated with the time to exhaustion ($R = 0.02$, $P = 0.96$ and $R = 0.17$, $P = 0.68$, respectively). Moreover, the normalized changes of C_r at the 33% - 66% interval of the time to exhaustion were negatively correlated with the change in F_{zmax} ($R = j0.86$, $P = 0.001$) and positively correlated with the changes in $\$L$ ($R = 0.67$, $P < 0.05$). Absolute and normal-

ized values of oxygen uptake and cost of running are presented in Table 1.

DISCUSSION

The first purpose of this study was to characterize in elite triathletes the effect of fatigue in leg-spring behavior during an exhaustive run. Because of the close relationships between running velocity and leg stiffness (6,27), the run was imposed here at a constant pace (95% of $v \cdot O_{2max}$). One of the main results was that leg stiffness decreased with fatigue. This change in spring - mass behavior agrees with previous sprint (20) or long distance (13) investigations. However, in these studies, the reduced leg stiffness was primarily related with the leg compression increase. On the contrary, the present results reveal that the vertical force is the most associated with the adaptations of leg stiffness, leg compression remaining constant through the fatiguing run.

Regarding the vertical stiffness, no change was observed. This finding differs from the abovementioned studies in which this parameter was reported to decrease with time (13,16,20,29). The discrepancy between these results could be explained by the similar decrease in $\$y$ and F_{zmax} observed in this study ($\approx 10\%$). These results are all the same consistent with those reported by Millet et al. (28), who suggested that elite triathletes partly compensate for the effects of fatigue by decreasing the maximal vertical displacement of the COM during foot contact.

It could be assumed that the alteration of the neuromuscular functioning as a result of the fatigue induced by a severe running exercise directly influences the leg-spring behavior. Among the stride mechanical characteristics, the vertical force is the most affected by this stiffness adaptation. This assumption is firstly supported by EMG studies investigating the effect of fatigue during running (31) or jumping exercises (5,24,34). For example, Nummela et al. (31) tested well-trained runners during a self-paced 5-km run. They showed that better performances were observed in runners whose level of muscle recruitment remains stable or just slightly decreases during the 5-km run. In jumping conditions, Kuitunen et al. (24) found that the leg stiffness

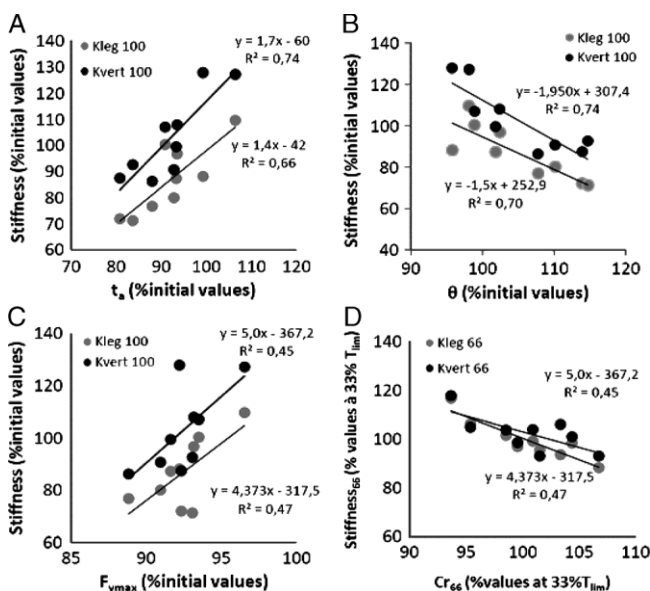


FIGURE 3—Scatterplots with correlations between normalized changes in k_{leg} and k_{vert} stiffness and normalized changes in (A) aerial time (t_a), (B) angle of the spring leg at touchdown (θ), (C) maximal horizontal reaction force (F_{ymax}), and (D) energy cost of running (C_r). Changes were calculated between 10% and 100% of the time to exhaustion, except for C_r , which was calculated between 33% and 66% of the time to exhaustion.

was strongly related to the EMG changes in the lower limb. Although we did not perform EMG analyses, it is consistent to assume that the observed decrease in vertical reaction force was related to the neuromuscular capacity of the lower limbs. Second, it is also supported by the positive relationship between the normalized changes in maximal vertical forces (F_{zmax}) and the angle of the velocity vector at toe off (α). Interestingly, the subjects who exhibited the highest difficulties in sustaining great vertical force were those who flattened their COM trajectories. Figure 4 provides a schematic of the above-cited modifications of the SMM behavior with fatigue. This figure presents the mean modification in several parameters but does not account for the interindividual variability.

This quite large interindividual variability is partly explained by the different time courses of stiffness changes from one subject to another. For example, although four triathletes presented a decrease in k_{leg} greater than 10% after the first third of the time to exhaustion, three subjects presented a decrease less than 10% after the middle third and two subjects did not show any decrease. Regarding k_{vert} values, the individual time course was more progressive. Although for seven subjects k_{vert} fluctuated between T5% after the first third, only one subject remained in this range of variation at the end of the run. Indeed, four subjects presented an increase whereas four subjects presented a decrease in vertical stiffness, such as these eight subjects presented variations in this parameter higher than 10% at the end of the run. These great differences of the time course changes between subjects were previously observed for moderated-velocity/long-duration running (13,22). The abovementioned observations show that this is also true for a more severe intensity/shorter duration exhaustive run (Table 1 and Fig. 2).

The analysis of spatiotemporal parameters permits for greater insight into mechanisms described above that

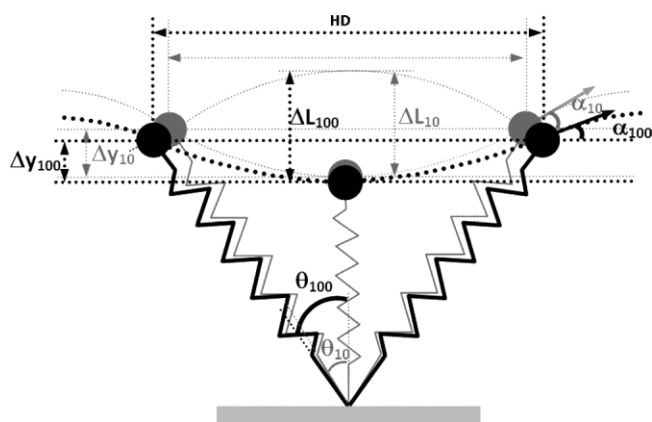


FIGURE 4—Schematic representation of the evolution of the SMM between the beginning (10% of the time to exhaustion, gray) and the end (100% of the time to exhaustion, black). α , angle of velocity vector at toe off; ΔL , leg compression; Δy , vertical displacement of the COM; θ , angle of the spring leg at touchdown; HD, horizontal distance of the COM during the contact phase.

allowed subjects to maintain a constant velocity despite fatigue. At constant velocity, contact time reflects the leg-spring angle at the moment of impact. Increasing the angle of the lower limb allowed the subjects to increase their horizontal COM distance during the contact phase. Furthermore, it might have allowed for the subject to maintain a constant horizontal impulse despite the decrease in neuromuscular capacity as a result of fatigue. This conclusion is supported by the fact that normalized changes in braking and propulsive impulses were positively correlated with normalized θ changes; in other words, the subjects who best maintained horizontal impulse were those who increased the most their leg-spring angle at the moment of impact. Moreover, negative relationships were observed between k_{vert} or k_{leg} and θ . Taken together, these results imply that changes of vertical and leg stiffness, via the increase in the leg-spring angle at impact, allow for maintaining the horizontal forces concomitantly with the onset of fatigue. However, it must be noticed that these findings do not take into account the changes in ankle, knee, and hip angles with fatigue. In running as well as in hopping conditions, it was shown that changes in lower limbs kinematics have substantial effects on the global musculoskeletal stiffness (1,21,27). Further studies are required to specifically analyze the contributions of these adaptations with the fatigue induced at this running velocity.

In nonfatigue status, it was shown that leg stiffness is positively related to step frequency (14). However, the present results show that k_{leg} decreased while f increased. As seen in the Results section, a significant increase in step frequency despite an increase in contact time was due to a greater decrease in aerial time. This result can explain the opposite changes observed between k_{leg} and f . Morin et al. (30) also reported that k_{leg} was more strongly associated with contact time than with stride frequency. As mentioned earlier, this increase in t_c could be due to a reduced capacity of the neuromuscular system to generate force rapidly or to tolerate impact forces (17). By examining subjects on an exhaustive 10-km run, Paavolainen et al. (33) concluded a failure of the muscle stiffness on the basis of i) relationships between the decreased preactivation and horizontal ground reaction forces and ii) longer contact times in the braking phases. It could be noticed that in response to central and/or peripheral physiological failure, beyond the parameters of the stance phase, the stiffness adaptation affects globally the stride characteristics. The present results have indeed shown that normalized changes in stiffness (both k_{leg} and k_{vert}) were strongly correlated not only with increases in contact time but also with decreases in aerial times. This would contribute to maintain a constant velocity in the later stages of the severe intensity exhaustive run.

During nonfatiguing protocols, Farley and Gonzalez (14) and Morin et al. (30) demonstrated that a leg stiffness adjustment is observed when different foot contact time (30) or stride frequency (14,30) is imposed. Nevertheless, the respective impact of a neuromuscular failure or of a central

regulatory process on the stiffness adaptation remained unclear under fatiguing conditions. Further investigations are required to identify whether the modifications in leg-spring stiffness are initially associated with deterioration in the neuromuscular functioning or with an anticipatory adjustment of the stride pattern with respect to the evolution of neuromuscular afferent feedbacks.

The second purpose of this study was to characterize how the changes in leg-spring behavior were related to the cost of running. From an energetic point of view, we observed that during the middle third of the time to exhaustion, the triathletes who presented highest decreases in stiffness values were also those who presented highest increases in C_r . This observation is in agreement with results obtained by numerous other studies (10,19,35) that showed that runners with greater leg compliance had greater cost of running. Furthermore, negative correlations were also observed between normalized changes in F_{zmax} and oxygen uptake. Our present study suggests that the adaptation of the leg stiffness as a result of fatigue leads to stride characteristics energetically less economical. However, the significant relationships

between k_{leg} , k_{vert} , and C_r between one-third and two-thirds of the run were found to not influence the subject's time to exhaustion.

In conclusion, the decrease in leg-spring stiffness during a severe intensity exhaustive run affects primarily the decrease in vertical force. The decrease in the velocity vector angle at takeoff allowed the subject 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. However, from an energetic point of view, runners with greatest increases of cost of running were those with greatest changes of stiffness as they fatigued during the run to exhaustion.

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