

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/329736652>

Analysis of the bouncing mechanism of running at different speeds and the relation with the three-phasic model of one elite middle-distance athlete

Poster · December 2018

CITATIONS

0

READS

131

4 authors:



Mario Núñez Lisboa

Universidad Finis Terrae

5 PUBLICATIONS 6 CITATIONS

[SEE PROFILE](#)



Arthur Dewolf

Université Catholique de Louvain - UCLouvain

42 PUBLICATIONS 265 CITATIONS

[SEE PROFILE](#)



Hermann Zbinden-Foncea

Universidad Finis Terrae

66 PUBLICATIONS 811 CITATIONS

[SEE PROFILE](#)



Jorge Cancino

Universidad Finis Terrae

60 PUBLICATIONS 145 CITATIONS

[SEE PROFILE](#)

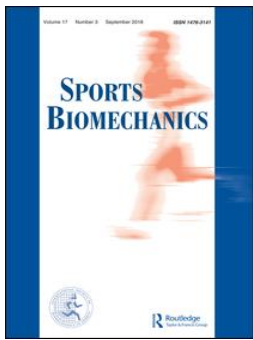
Some of the authors of this publication are also working on these related projects:



Postural control and EMG [View project](#)



beer and water consumption [View project](#)



Influence of sports background on the bouncing mechanism of running

M. Núñez Lisboa, LE Peñailillo, J. Cancino, H. Zbinden-Foncea & AH Dewolf

To cite this article: M. Núñez Lisboa, LE Peñailillo, J. Cancino, H. Zbinden-Foncea & AH Dewolf (2021): Influence of sports background on the bouncing mechanism of running, Sports Biomechanics, DOI: [10.1080/14763141.2021.1884284](https://doi.org/10.1080/14763141.2021.1884284)

To link to this article: <https://doi.org/10.1080/14763141.2021.1884284>



Published online: 05 Mar 2021.



Submit your article to this journal [↗](#)



View related articles [↗](#)



View Crossmark data [↗](#)



Influence of sports background on the bouncing mechanism of running

M. Núñez Lisboa^a, LE Peñailillo^a, J. Cancino^a, H. Zbinden-Foncea^{a,b} and AH Dewolf^{c,d} 

^aExercise Science Laboratory, School of Kinesiology, Faculty of Medicine, Santiago, Chile; ^bClinica Santa Maria, Santiago, Chile; ^cDepartment of Systems Medicine and Centre of Space Biomedicine, University of Rome Tor Vergata, Rome, Italy; ^dLaboratory of Biomechanics and Physiology of Locomotion, Institute of NeuroScience, Louvain-la-Neuve, Belgium

ABSTRACT

During running, the mechanical energy of the centre of mass of the body (COM) oscillates throughout the step like a spring-mass system, where part of its mechanical energy is stored during negative phases to be released during the following positive phases. This storage-release of energy improves muscle-tendon efficiency, which is related to lower-limb stiffness. This study explores the effect of sports background on the bouncing mechanism, by examining differences in stiffness and step spatiotemporal parameters between swimmers and football athletes. All athletes performed three consecutive running bouts on an instrumented treadmill at three different speeds (3.9, 4.4 and 5.0 m·s⁻¹). The ground reaction forces were recorded. Vertical stiffness and step spatiotemporal parameters were analysed and compared using a two-way ANOVA. Vertical stiffness of football players was on average 21.0 ± 1.1% higher than swimmers. The modification of step spatiotemporal parameters also suggests a more elastic rebound by increasing the stretch of tendons relative to muscle within muscle-tendon units in football players. Compared to swimmers, they (1) decrease the effective contact time by 9.7 ± 2.4% and (2) decrease the duration of the push by 15.0 ± 6.4%, suggesting that background training adaptations influence spring-mass behaviour during running.

ARTICLE HISTORY

Received 14 May 2020
Accepted 26 January 2021

KEYWORDS

Spring-mass system;
muscle-tendon efficiency;
biomechanics; training
experience; running
economy

Introduction

During running, the centre of mass of the body (COM) oscillates throughout the step, whilst the lower-limb acts like a single linear spring bouncing vertically on the ground (Cavagna et al., 1964). Therefore, the COM motion has been modelled as a spring-mass system bouncing on the ground (Cavagna et al., 1976). During this bounce, the muscle-tendon units (MTU) of the supporting lower limb undergo stretch-shortening cycles during which part of the mechanical energy of the COM stored during the negative work phase is released during the next positive work phase (Cavagna et al., 1988) of a step. This storage-release of elastic potential energy by the MTUs increases the muscular efficiency above the maximum efficiency of the

conversion of chemical energy into positive work by the unstretched contractile machinery of skeletal muscles (Dickinson, 1929; Willems et al., 1995).

The bouncing mechanism of running can be characterised by the vertical stiffness of the spring-mass system (k_{vert}), which reflects the stiffness of the entire lower-limb (McMahon & Cheng, 1990). When running speed increases, k_{vert} increases linearly (Brughelli & Cronin 2008b; Dewolf et al., 2016; da Rosa et al., 2019). This increase has been related to the increase of the muscle-tendon efficiency as running speed increases (Lejeune et al., 1998). This relationship has been supported by various studies. Takahashi and Nabekura (2017) showed that a smaller metabolic cost of running was associated with greater k_{vert} in triathletes. Also, when running on sand, k_{vert} is reduced (Dewolf et al., 2019), resulting in a greater oxygen consumption despite only a slight increase of mechanical work (Lejeune et al., 1998). Taken together, this suggests that the storage-release of elastic energy, and in turn the MTU efficiency, is greater in runners that have a greater vertical stiffness (da Rosa et al., 2019).

As hypothesised by Cavagna (2009), the modification of k_{vert} may result in a different spatiotemporal organisation of the step. Indeed, the spring-mass system oscillates around an equilibrium point at which the vertical acceleration of the COM (a_v) is nil (Cavagna et al., 1997). The step period can thus be divided into two parts: the first part (t_{ce}) during which $a_v > 0$ (lower part of the oscillation), and the second part (t_{ae}) during which $a_v \leq 0$ (upper part of the oscillation). When running at slow speeds, k_{vert} is small, and the rebound is symmetric (i.e. $t_{\text{ce}} \sim t_{\text{ae}}$). According to Cavagna et al. (1997), runners adopt a $t_{\text{ce}}/t_{\text{ae}}$ ratio of 1 at speeds less than about $3.1 \text{ m}\cdot\text{s}^{-1}$ to maximise the muscular efficiency. Such symmetric rebound seems to occur when the stretch of muscle is greater than that of the tendon within MTUs (Cavagna, 2006, 2009). Indeed, at slow running speeds, the period during which muscle performs positive work (t_{push}) is greater than the period during which muscle performs negative work (t_{brake}). This difference in time is due to the greater muscular force exerted during eccentric contraction (i.e. negative work phase), supporting an important contribution of the skeletal muscle to the work production (Cavagna, 2006; Dewolf & Willems, 2017, 2019; Mesquita et al., 2020).

As running speed increases, the lower-limb muscle activation and the vertical push on the ground also increase (Arampatzis et al., 1999; Blickhan, 1989; Cavagna, 2009), resulting in a higher k_{vert} . Since the vertical momentum gained during t_{ce} must equal that lost during t_{ae} , t_{ae} becomes longer than t_{ce} and the rebound is no longer symmetric. A ratio $t_{\text{ce}}/t_{\text{ae}} < 1$ has the physiological advantage of reducing the step frequency and thereby limiting the power spent to reset the limbs at each step (Cavagna et al., 1997). In turn, the greater k_{vert} results in a $t_{\text{push}} = t_{\text{brake}}$, which suggests that the work contribution of the contractile machinery is progressively substituted by the storage and release of elastic energy from non-contractile structures (e.g., tendons) (Cavagna, 2006, 2009). In sum, increasing k_{vert} with running speed results in modification of the spatiotemporal organisation of the running step: the $t_{\text{ce}}/t_{\text{ae}}$ ratio decreases whereas the $t_{\text{brake}}/t_{\text{push}}$ ratio increases, reflecting a more elastic rebound.

Recently, da Rosa et al. (2019) analysed 38 endurance runners, divided into two groups based on their performance in a 3000 m test (fastest versus slowest runners). By analysing k_{vert} and the spatiotemporal organisation of the step, they showed that the storage-release of elastic energy was greater in faster runners as compared to

slower runners. These authors concluded that more experienced runners demonstrated a better use of elastic components of the MTUs. Thus, it is plausible to think that training may affect leg stiffness as endurance athletes show higher leg stiffness than untrained subjects (Hobara et al., 2010; Spurrs et al., 2003). Also, k_{vert} is higher in power than endurance athletes (Hobara et al., 2008) and plyometric training also increases stiffness (Cornu et al., 1997). These results suggest that both training and athletics experience may determine k_{vert} , potentially modifying the role of the elastic and contractile components of the MTUs during running. A better understanding of how training and experience affect k_{vert} is warranted for the identification of the optimal stiffness for a range of sports. In particular, strength and conditioning coaches could ensure that training is designed to reach the optimal stiffness for successful athletic performance, using for example, plyometric or power training (J. McMahon et al., 2012). In addition, the identification of a relation between k_{vert} and spatiotemporal parameters of the running step may help in the assessment of training-induced plasticity (Millett et al., 2018), based on simple mechanical parameters.

Therefore, the aim of this study was to examine differences in bouncing mechanisms between athletes that use the muscles as a motor and brake and athletes that use muscles primarily as a motor (Figure 1). To do that, we compared the running pattern of football players (SOC) and swimmers (SWI), whilst running on a treadmill at three different speeds. We hypothesised that, since swimmers do not perform much running or stretch-shortening cycle contractions of the lower-limb muscles and mainly realise concentric contraction during training, their lower-limb stiffness will be smaller than football players. It is also expected that swimmers would exhibit greater $t_{\text{ce}}/t_{\text{ae}}$ ratios and lower $t_{\text{brake}}/t_{\text{push}}$ ratios as compared to football players.

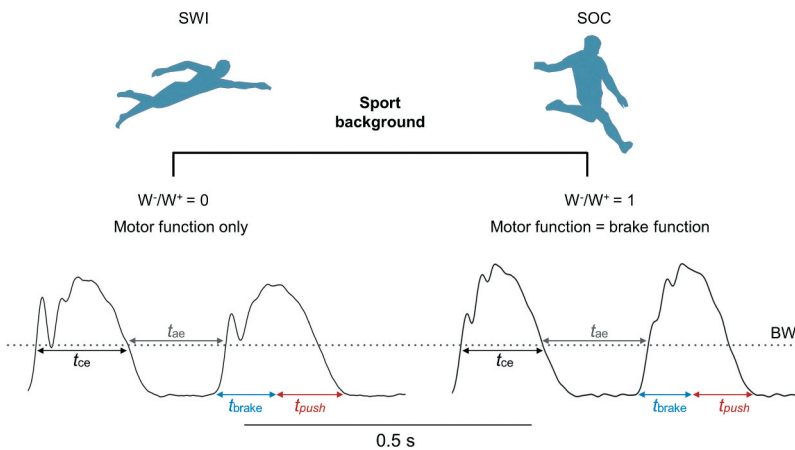


Figure 1. Study design. *Top*—Schematic representation of the study design in which the bouncing mechanism of swimmers, using primarily muscles as a motor doing positive work [W^+] in their sport activity, is compared to that of football players, using muscles both as a motor and as a brake in their sport activity (doing as much positive [W^+] than negative [W^-] work). *Bottom*—Typical force time traces of a swimmer and of a football player while running at 4.44 m s^{-1} . The horizontal dotted line corresponds to body weight (BW) and divides the running step into two parts: the effective contact time (t_{ce}) when $F_v > \text{BW}$ and the effective aerial time (t_{ae}) when $F_v < \text{BW}$. The contact time is also divided into two parts: the duration of the phase during which the COM is accelerated (t_{push}) and decelerated (t_{brake}).

Methods

Participants

Six professional male SOC and six male junior elite SWI participated in this study (Anthropometric characteristics are shown in Table 1). It is reported that SOC and SWI have trained at least 10 specific training sessions per week the year before the experiment. Note that age difference between groups does not affect the bouncing mechanism, since running in humans attain the adult mature bouncing mechanism in their teens (Legramandi et al., 2013). Indeed, Schepens et al. (1998) and Legramandi et al. (2013) did not find any significant difference between $t_{\text{brake}}/t_{\text{push}}$ and $t_{\text{ce}}/t_{\text{ae}}$ between subjects from 16 and up to 27 years old (see Fig. S1 for a comparison with age). There were no significant differences of height and mass between groups, but the BMI of SWI was smaller than SOC. The sample size was estimated a priori based in the difference of 15.6% in the contact time (effect size = 1.7) between distance athletes and power athletes reported in a previous study (Hobara et al., 2008). Considering a power analysis of 0.85 (1- beta) and considering one-way ANOVA with an alpha level of 0.05, 6 subjects per group would be sufficient. All subjects signed an informed consent form and the study was approved by the Institutional Ethics Committee (resolution 37/2018) for Human Research at Finis Terrae University and performed according the Helsinki declaration.

Table 1

Table 1. Anthropometric characteristics (mean $\pm$ SD) of the participants.

	SOC	SWI
	Mean $\pm$ SD	Mean $\pm$ SD
Age (years)	22.9 $\pm$ 1.4	16.5 $\pm$ 0.8
Body mass (kg)	72.8 $\pm$ 6.4	65.5 $\pm$ 4.6
Height (m)	1.72 $\pm$ 0.06	1.76 $\pm$ 0.03
BMI (kg·m ⁻²)	24.4 $\pm$ 1.2	21.1 $\pm$ 1.4

Means and standard deviations of age, body mass, height and body mass index (BMI) of swimmers (SWI) and football players (SOC).

Study design

All athletes performed a 10 minute warm-up, including running on the treadmill at $\sim 2.8 \text{ m s}^{-1}$. Once warmed-up, the participants ran on an instrumented treadmill (Treadmill: Hp/Cosmos, Germany; Force platform: Arsalis, Belgium) at three different speeds (3.9, 4.4 and $5.0 \text{ m} \cdot \text{s}^{-1}$, respectively 14, 16 and 18 km h^{-1}) for 1 minute, with a 2 minute rest between each speed to avoid a possible fatigue effect. These speeds, higher than typical endurance running speeds, were considered because the variability of spatiotemporal parameters between subjects decreases with increasing speed (Lussiana et al., 2019). The vertical (F_v), lateral and horizontal ground reaction forces were

recorded at 1000 Hz during the final 10 seconds of each running bout. The acceleration (a), velocity and displacement of the COM and the energy done to move the COM relative to the ground (E_{COM}) were then computed from the ground reaction force (GRF) (Dewolf et al., 2017; Willems & Gosseye, 2013). In short, the fore-aft and vertical acceleration of the COM were respectively computed as $a_f = F_f/m$ and $a_v = (F_v - BW)/m$, where m is the subject's body mass and BW the subject's body weight. The instantaneous velocity in the fore-aft (v_f) and vertical (v_v) directions were obtained by integration of a_f and a_v plus an integration constant. The constants were chosen to make the average v_f over each stride equal to the velocity of the treadmill belt and the average v_v over each stride equal to zero. A second integration of the vertical velocity yields the vertical displacement of the COM (S_v). From the velocity and displacement of the COM, its kinetic (E_k), potential (E_p) and the total energy done to move the COM were computed as follow:

$$E_p = mgS_v,$$

$$E_k = \frac{m(v_v^2 + v_f^2)}{2},$$

$$E_{COM} = E_k + E_p,$$

where m is the mass of the subject and g is the gravity.

Measurements of the bouncing mechanism of running

Spatiotemporal organisation of the steps

Steps were divided according to the F_v -time curves at each speed (Figure 1). The effective aerial time (t_{ae}) was the period during which the vertical force $F_v < BW$ (Cavagna et al., 1988) and the effective contact time (t_{ce}) was the period during which $F_v \geq BW$ (Figure 1). The step period (T) was then computed as $T = t_{ce} + t_{ae}$. The period t_{push} and t_{brake} were defined as the duration of the positive and of the negative E_{COM} phases, respectively.

Vertical stiffness

At each step, the second peak (F_{max}) of F_v (also called 'active' peak (Lieberman et al., 2010)) was measured. The range of vertical displacement of the COM S_v during t_{ce} (Δy) was then measured. Finally, the vertical stiffness k_{vert} was computed as ((Butler et al., 2003)): $k_{vert} = F_{max}/\Delta y$

Statistical analysis

For each dependent variable the normality was assumed based on D'Agostino-Pearson test. A two-way ANOVA with post-hoc Fisher's Least Significant

Difference (LSD) correction was performed to evaluate the individual and interaction effects of speed and groups. All statistical analyses were performed using GraphPad 6 software (Prism, California, USA) with an alpha level set at 0.05.

Results

Table 2

Vertical stiffness

The vertical stiffness k_{vert} was significantly smaller in SWI than in SOC across all speeds ($p = 0.016$). On average, k_{vert} was $21.0 \pm 1.1\%$ smaller in SWI (Table 2). In both groups, k_{vert} increased similarly with speed (speed: $p < 0.001$; interaction: $p = 0.187$). The modification of k_{vert} could be explained by a difference in F_{max} , or Δy , or a combination of both. The greater k_{vert} in SOC was due to a greater F_{max} ($\sim 10\%$; $p = 0.010$) and to a smaller Δy ($\sim 10\%$; $p < 0.0001$) in SOC. In both groups, F_{max} and Δy increased similarly with speed (speed: $p < 0.001$; interaction: $p = 0.187$).

Table 2. Vertical stiffness of the running step.

	Speed	SWI		SOC		% difference	<i>p</i>
		Mean	SD	Mean	SD		
k_{vert} (N kg ⁻¹ m ⁻¹)	3.88 m s ⁻¹	229.0	7.1	279.4	16.0	22%	*0.016
	4.44 m s ⁻¹	272.9	7.2	327.7	21.8	20%	*0.039
	5.00 m s ⁻¹	316.8	9.5	386.3	20.2	22%	*0.017
F_{max} (N kg ⁻¹)	3.88 m s ⁻¹	24.4	0.3	26.3	0.6	8%	*0.035
	4.44 m s ⁻¹	25.0	0.4	27.1	0.5	9%	*0.014
	5.00 m s ⁻¹	25.8	0.3	28.3	0.5	10%	*0.003
Δy (m)	3.88 m s ⁻¹	0.11	0.04	0.09	0.03	12%	*0.017
	4.44 m s ⁻¹	0.09	0.05	0.08	0.02	10%	*0.039
	5.00 m s ⁻¹	0.08	0.03	0.07	0.02	10%	0.123

Means and standard deviations of vertical stiffness (k_{vert}), second peak of vertical force (F_{max}) and amplitude of vertical displacement of the COM during effective contact time (Δy) in swimmers (SWI) and football players (SOC), at three different running speeds. The *p-values* (right column) correspond to independent sample Student t-test, where the * indicates a significant effect of sport backgrounds ($p < 0.05$).

Spatiotemporal parameters of the running step

At all speeds and in both groups, t_{ae} was greater than t_{ce} (Figure 2B). As speed increased, t_{ce} and, to a much smaller extent, t_{ae} decreased ($p < 0.001$) in both groups. When comparing the two groups across all speeds, t_{ce} was on average $9.7 \pm 2.4\%$ smaller in SOC as compared to SWI ($p < 0.001$) whereas t_{ae} was not significantly different ($p > 0.374$). As a result, the ratio $t_{\text{ce}}/t_{\text{ae}}$ was smaller in SOC and T was greater in SWI than in SOC (Figure 2A; $p < 0.001$).

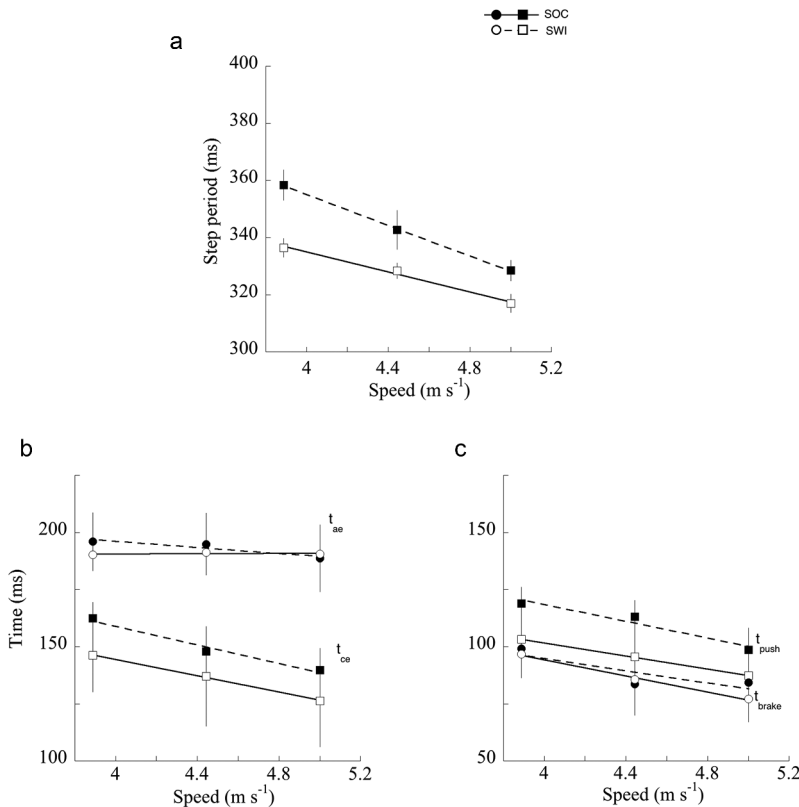


Figure 2. Spatiotemporal organisation of the step. Step duration (A), effective contact (squares— t_{ce}) and the effective aerial (circles— t_{ae}) time (B), and the duration of the acceleration (squares— t_{push}) and deceleration (circles— t_{brake}) phases of the COM (C). In each plot, the filled symbols indicate the data of swimmers ($n = 6$) and the open symbols those of football players ($n = 6$). Symbols and bars represent the mean and the standard deviations (when the length of the bar exceeds the size of the symbol). The interrupted and continuous lines were drawn through the experimental data (weighted mean, Kaleidagraph 4.5).

At all speeds and in both groups, t_{push} was greater than t_{brake} (Figure 2C). As speed increased, t_{brake} and t_{push} decreased ($p < 0.001$) to a similar extent in both groups (interaction: $p = 0.713$). When comparing SOC with SWI, t_{push} was on average $15.0 \pm 6.4\%$ greater in the SWI group ($p = 0.016$) whereas t_{brake} was not significantly different between groups. As a result, the ratio t_{brake}/t_{push} was greater in SOC ($p < 0.001$) at all speeds.

Discussion and implications

The aim of this study was to compare the bouncing mechanism of running in athletes of different sport backgrounds and running experience. In particular, we compared athletes using muscles as motors and as brakes during activity (football players—SOC) with athletes using muscles primarily as motors (swimmers—SWI) (Figure 1). We hypothesised SOC to have a better storage-release of elastic energy as compared to SWI. Our

hypothesis was confirmed since the elastic rebound, reflected by k_{vert} and by the spatio-temporal organisation of the step, was significantly greater in the SOC group.

Our primary finding was that SOC have greater k_{vert} than SWI (Table 2). This difference is due to a smaller vertical displacement of the COM and a greater F_{max} in SOC in comparison with SWI (Table 2). A greater k_{vert} has been related to the enhancement of the MTUs efficiency (Lejeune et al., 1998). This relation suggests that muscular efficiency of football players is greater than swimmers, potentially resulting in smaller oxygen consumption when running at the same speed. Indeed, reduced running economy (i.e. greater oxygen consumption) has been associated with lower lower-limb stiffness (Arampatzis et al., 1999; Heise & Martin, 1998; Morin et al., 2006; Takahashi & Nabekura, 2017). Such results may be explained by the fact that greater stiffness increase the elastic contribution, increasing the MTU efficiency and reducing the metabolic cost (Cavagna, 2009; Lejeune et al., 1998; Sasaki & Neptune, 2006).

In 2009, Cavagna shed light on a ‘possible relation’ between the spatiotemporal organisation of the step and k_{vert} . Here we also show that the modifications of the elastic rebound of the body were reflected in the spatiotemporal parameters of the running step. Indeed, we observed that the ratios $t_{\text{ce}}/t_{\text{ae}}$ and $t_{\text{brake}}/t_{\text{push}}$ accurately reflect the modifications of the bouncing mechanism of running. Recently, da Rosa et al. (2019) also demonstrated that these ratios may be used to differentiate the parameters of the mass-spring system in athletes, information not reflected in the contact/aerial time asymmetry. In particular, they highlighted modifications of $t_{\text{ce}}/t_{\text{ae}}$ without modifications of $t_{\text{brake}}/t_{\text{push}}$ between slower and faster performing athletes in a 3000 m running performance. While da Rosa et al. (2019) were the first to demonstrate modification of spatiotemporal parameters of the bouncing mechanism related to sport performance, they analysed athletes with relative homogeneous running experience and training, with most likely similar muscular force capabilities. By comparing groups with heterogeneous sport experience (Figure 1), we showed here that also the modifications of $t_{\text{brake}}/t_{\text{push}}$ may be used to detect the contribution of muscle to the length change of the MTUs. Since classic spatiotemporal parameters, as contact and flight durations, usually used in the literature (Morin et al., 2007; Pantoja et al., 2016) are less sensitive to detect differences in running mechanics (da Rosa et al., 2019), future studies investigating running performance together with the spring-mass behaviour should consider the use of $t_{\text{ce}}/t_{\text{ae}}$ and $t_{\text{brake}}/t_{\text{push}}$.

The optimisation of the bouncing mechanism of running may be explained by various factors. First, training may affect MTUs stiffness. For example, k_{vert} is higher in power-trained than in endurance athletes (Hobara et al., 2008) or untrained subjects (Hobara et al., 2010; Spurrs et al., 2003). In addition, specific training, such as plyometric training, also results in greater k_{vert} (Cornu et al., 1997) and k_{vert} is correlated with eccentric strength (Li et al., 2019). Such correlations may partly explain why athletes performing mainly concentric contractions (SWI, Figure 1) have lower k_{vert} than those using muscles as motors and as brakes (SOC). Secondly, based on lower limb coordination, Bianchi et al. (1998) showed that trained subjects can exploit better the dynamic coupling between segments to save mechanical energy than untrained subjects. It is, therefore, plausible that specific training may affect the lower limb intersegmental coordination to allow an optimised bouncing mechanism. Finally, muscle coordination may also be adapted following training. For example, by

analysing the influence of sports background on leg muscle coordination in vertical jumps, Eloranta (2003) showed that prolonged training causes the central nervous system to adjust muscle coordination according to the demands of that activity. Therefore, it is reasonable to believe that swimmers running behaviour could be influenced by their previous learned skills. More recently, it has been shown that with increasing running experience, specific patterns of muscle coordination appear. The presence of those patterns were correlated with the progressive enhancement of bouncing mechanism of running with experience (Cheung et al., 2020). Such results suggest that training induces fine-tuning of muscle coordination, resulting in an efficient gait.

This study has some limitations inherent to the methods and protocol used. We used a whole-body approach to gain insights into the realisation of human gait. This approach provides results at the level of the COM mechanics and the relative simplicity of the templates—the spring-mass model—in comparison with biological organism, only allows interpretation of the global behaviour. In addition, the small sample size may be considered as a limitation. Even though the group size satisfied a population size for a statistical analysis, future research should compare larger groups of athletes with various training experience to extend the present results. A larger sample size should also be necessary to achieve reliable results concerning other potential influencing factor, such as the body mass index. Moreover, the training experience of our subjects more than one year before the experiment was not investigated. Despite those limitations, our results give valuable information on the directions that need to be taken for researchers and practitioners in the future (Brughelli & Cronin, 2008a). In particular, longitudinal monitoring of the modification of bouncing mechanism with training may help to understand how athletes progressively have a better use of elastic components, together with a reorganisation of muscle recruitment patterns (Cheung et al., 2020). Moreover, monitoring the reorganisation of spatiotemporal parameters may help identify differences in the bouncing mechanism, when stiffness cannot be evaluated directly.

Conclusion

In conclusion, our results suggest that athletes' training and competition history in a sport requiring running component demonstrate a better use of elastic components than athletes not performing much running or stretch-shortening cycle contractions of the lower-limb muscles during training. Future studies should be designed to understand how the running pattern is progressively adjusted with long-term training specificity, in order to improve the storage-release of elastic energy in MTUs.

List of Abbreviations

a_f , v_f	fore-aft acceleration and velocity of the COM
a_v , v_v , S_v	vertical acceleration, velocity and displacement of the COM
BW	body weight
COM	centre of mass
E_k , E_p , E_{COM}	kinetic, potential and total mechanical energy of the COM

F_f, F_v	fore-aft and vertical component of the GRF
GRF	ground reaction force
k_{vert}	vertical stiffness
MTU	muscle-tendon unit
F_{max}	maximum of F_v
$t_{\text{ce}}, t_{\text{ae}}$	effective contact and aerial time
$t_{\text{push}}, t_{\text{brake}}$	duration of the COM positive and negative work
Δy	range of S_v during t_{ce}
MTU	efficiency the ability to transform chemical energy into muscle work

Disclosure statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

ORCID

AH Dewolf  <http://orcid.org/0000-0003-1498-3987>

References

- Arampatzis, A., Brüggemann, G. P., & Metzler, V. (1999). The effect of speed on leg stiffness and joint kinetics in human running. *Journal of Biomechanics*, 32(12), 1349–1353. [https://doi.org/10.1016/s0021-9290\(99\)00133-5](https://doi.org/10.1016/s0021-9290(99)00133-5)
- Bianchi, L., Angelini, D., & Lacquaniti, F. (1998). Individual characteristics of human walking mechanics. *Pflügers Archiv European Journal of Physiology*, 436(3), 343–356. <https://doi.org/10.1007/s004240050642>
- Blickhan, R. (1989). The spring-mass model for running and hopping. *Journal of Biomechanics*, 22(11–12), 1217–1227. [https://doi.org/10.1016/0021-9290\(89\)90224-8](https://doi.org/10.1016/0021-9290(89)90224-8)
- Brughelli, M., & Cronin, J. (2008a). A review of research on the mechanical stiffness in running and jumping: Methodology and implications. *Scandinavian Journal of Medicine & Science in Sports*, 18(4), 417–426. <https://doi.org/10.1111/j.1600-0838.2008.00769.x>
- Brughelli, M., & Cronin, J. (2008b). Influence of running velocity on vertical, leg and joint stiffness: Modelling and recommendations for future research. *Sports Medicine*, 38(8), 647–657. <https://doi.org/10.2165/00007256-200838080-00003>
- Butler, R. J., Crowell, H. P., & Davis, I. M. C. (2003). Lower extremity stiffness: Implications for performance and injury. *Clinical Biomechanics*, 18(6), 511–517. [https://doi.org/10.1016/S0268-0033\(03\)00071-8](https://doi.org/10.1016/S0268-0033(03)00071-8)
- Cavagna, G. A., Saibene, F. P., & Margaria, R. (1964). Mechanical work in running. *Journal of Applied Physiology*, 19, 249–256. <https://doi.org/10.1152/jappl.1964.19.2.249>
- Cavagna, G. A., Thys, H., & Zamboni, A. (1976). The sources of external work in level walking and running. *The Journal of Physiology*, 262(3), 639–657. <https://doi.org/10.1113/jphysiol.1976.sp011613>
- Cavagna, G. A., Franzetti, P., & Heglund, N. C. (1988). The determinants of the step frequency in running, trotting and hopping in man and other vertebrates. *Physiology*, 1988, 81–92. <https://doi.org/10.1113/jphysiol.1988.sp017069>
- Cavagna, G. A., Mantovani, M., Willems, P. A., & Musch, G. (1997). The resonant step frequency in human running. *Pflügers Archiv: European Journal of Physiology*, 434(6), 678–684. <https://doi.org/10.1007/s004240050451>
- Cavagna, G. A. (2006). The landing-take-off asymmetry in human running. *The Journal of Experimental Biology*, 209(Pt 20), 4051–4060. <https://doi.org/10.1242/jeb.02344>

- Cavagna, G. A. (2009). The two asymmetries of the bouncing step. *European Journal of Applied Physiology*, 107(6), 739–742. <https://doi.org/10.1007/s00421-009-1179-2>
- Cheung, V. C. K., Cheung, B. M. F., Zhang, J. H., Chan, Z. Y. S., Ha, S. C. W., Chen, C.-Y. C., & Cheung, R. T. H. (2020). Plasticity of muscle synergies through fractionation and merging during development and training of human runners. *Nat Commun*, 11, 4356. <https://doi.org/10.1038/s41467-020-18210-4>
- Cornu, C., Almeida Silveira, M. I., & Goubel, F. (1997). Influence of plyometric training on the mechanical impedance of the human ankle joint. *European Journal of Applied Physiology and Occupational Physiology*, 76(3), 282–288. <https://doi.org/10.1007/s004210050249>
- da Rosa, R. G., Oliveira, H. B., Gomeñuka, N. A., Masiero, M. P. B., da Silva, E. S., Zanardi, A. P. J., de Carvalho, A. R., Schons, P., & Peyré-Tartaruga, L. A. (2019). Landing-takeoff asymmetries applied to running mechanics: A new perspective for performance. *Frontiers in Physiology*, 10, 415. <https://doi.org/10.3389/fphys.2019.00415>
- Dewolf, A. H., Peñailillo, L. E., & Willems, P. A. (2016). The rebound of the body during uphill and downhill running at different speeds. *The Journal of Experimental Biology*, 219, 2276–2288. <https://doi.org/10.1242/jeb.142976>
- Dewolf, A. H., Ivanenko, Y. P., Lacquaniti, F., & Willems, P. A. (2017). Pendular energy transduction within the step during human walking on slopes at different speeds. *PloS One*, 12(10). <https://doi.org/10.1371/journal.pone.0186963>
- Dewolf, A. H., & Willems, P. A. (2017). A collision-based analysis of the landing-takeoff asymmetry during running. *Computer Methods in Biomechanics and Biomedical Engineering*, 20(sup1), 65–66. <https://doi.org/10.1080/10255842.2017.1382863>
- Dewolf, A. H., Lejeune, T. M., & Willems, P. A. (2019). The on-off ground asymmetry during running on sand. *Computer Methods in Biomechanics and Biomedical Engineering*, 22(suppl 1), 325–327. <https://doi.org/10.1080/10255842.2020.1714917>
- Dewolf, A. H., & Willems, P. A. (2019). Running on a slope: A collision-based analysis to assess the optimal slope. *Journal of Biomechanics*, 83, 298–304. <https://doi.org/10.1016/j.jbiomech.2018.12.024>
- Dickinson, S. (1929). The efficiency of bicycle-peddalling, as affected by speed and load. *The Journal of Physiology*, 67(3), 242–255. <https://doi.org/10.1113/jphysiol.1929.sp002565>
- Eloranta, V. (2003). Influence of sports background on leg muscle coordination in vertical jumps. *Electromyography and Clinical Neurophysiology*, 43(3), 141–156.
- Heise, G. D., & Martin, P. E. (1998). “Leg spring” characteristics and the aerobic demand of running. *Medicine and Science in Sports and Exercise*, 30(5), 750–754. <https://doi.org/10.1097/00005768-199805000-00017>
- Hobara, H., Kimura, K., Omuro, K., Gomi, K., Muraoka, T., Iso, S., & Kanosue, K. (2008). Determinants of difference in leg stiffness between endurance- and power-trained athletes. *Journal of Biomechanics*, 41(3), 506–514. <https://doi.org/10.1016/j.jbiomech.2007.10.014>
- Hobara, H., Kimura, K., Omuro, K., Gomi, K., Muraoka, T., Sakamoto, M., & Kanosue, K. (2010). Differences in lower extremity stiffness between endurance-trained athletes and untrained subjects. *Journal of Science and Medicine in Sport*, 13(1), 106–111. <https://doi.org/10.1016/j.jsams.2008.08.002>
- Legramandi, M. A., Schepens, B., & Cavagna, G. A. (2013). Running humans attain optimal elastic bounce in their teens. *Scientific Reports*, 3, 1310. <https://doi.org/10.1038/srep01310>
- Lejeune, T. M., Willems, P. A., & Heglund, N. C. (1998). Mechanics and energetics of human locomotion on sand. *The Journal of Experimental Biology*, 201(Pt 13), 2071–2080.
- Li, F., Newton, R. U., Shi, Y., Sutton, D., & Ding, H. (2019). Correlation of eccentric strength, reactive strength, and leg stiffness with running economy in well-trained distance runners. *Journal of Strength and Conditioning Research*. <https://doi.org/10.1519/JSC.0000000000003446>
- Lieberman, D. E., Venkadesan, M., Werbel, W. A., Daoud, A. I., D’Andrea, S., Davis, I. S., Mang’Eni, R. O., & Pitsiladis, Y. (2010). Foot strike patterns and collision forces in habitually barefoot versus shod runners. *Nature*, 463(7280), 531–535. <https://doi.org/10.1038/nature08723>

- Lussiana, T., Patoz, A., Gindre, C., Mourot, L., & Hébert-Losier, K. (2019). The implications of time on the ground on running economy: Less is not always better. *Journal of Experimental Biology*, 222. <https://doi.org/10.1242/jeb.192047>
- McMahon, T. A., & Cheng, G. C. (1990). The mechanics of running: How does stiffness couple with speed? *Journal of Biomechanics*, 23(Suppl 1), 65–78. [https://doi.org/10.1016/0021-9290\(90\)90042-2](https://doi.org/10.1016/0021-9290(90)90042-2)
- McMahon, J., Comfort, P., & Pearson, S. (2012). Lower limb stiffness: Effect on performance and training considerations. *Strength and Conditioning Journal*, 34, 94–101. <https://doi.org/10.1519/SSC.0b013e3182781b4e>
- Mesquita, R. M., Dewolf, A. H., Catavittello, G., Osgnach, C., Di Prampero, P. E., & Willems, P. A. (2020). The bouncing mechanism of running against hindering, or with aiding traction forces: A comparison with running on a slope. *Eur J Appl Physiol*, 120, 1575–1589. <https://doi.org/10.1007/s00421-020-04379-5>
- Millett, E. L., Moresi, M. P., Watsford, M. L., Taylor, P. G., & Greene, D. A. (2018). Variations in lower body stiffness during sports-specific tasks in well-trained female athletes. *Sports Biomechanics*, 20(1), 22–37. <https://doi.org/10.1080/14763141.2018.1521466>
- Morin, J.-B., Jeannin, T., Chevallier, B., & Belli, A. (2006). Spring-mass model characteristics during sprint running: Correlation with performance and fatigue-induced changes. *International Journal of Sports Medicine*, 27(2), 158–165. <https://doi.org/10.1055/s-2005-837569>
- Morin, J. B., Samozino, P., Zameziati, K., & Belli, A. (2007). Effects of altered stride frequency and contact time on leg-spring behavior in human running. *Journal of Biomechanics*, 40(15), 3341–3348. <https://doi.org/10.1016/j.jbiomech.2007.05.001>
- Pantoja, P. D., Morin, J. B., Peyré-Tartaruga, L. A., & Brisswalter, J. (2016). Running energy cost and spring-mass behavior in young versus older trained athletes. *Medicine and Science in Sports and Exercise*, 48(9), 1779–1786. <https://doi.org/10.1249/MSS.0000000000000959>
- Sasaki, K., & Neptune, R. R. (2006). Muscle mechanical work and elastic energy utilization during walking and running near the preferred gait transition speed. *Gait & Posture*, 23(3), 383–390. <https://doi.org/10.1016/j.gaitpost.2005.05.002>
- Schepens, B., Willems, P. A., & Cavagna, G. A. (1998). The mechanics of running in children. *The Journal of Physiology*, 509(3), 927–940. <https://doi.org/10.1111/j.1469-7793.1998.927bm.x>
- Spurrs, R. W., Murphy, A. J., & Watsford, M. L. (2003). The effect of plyometric training on distance running performance. *European Journal of Applied Physiology*, 89(1). <https://doi.org/10.1007/s00421-002-0741-y>
- Takahashi, K., & Nabekura, Y. (2017). Relationship between performance and vertical stiffness in triathlon running during a competition. *ISBS Proceedings Archive*, 35, article 278.
- Willems, P. A., Cavagna, G. A., & Heglund, N. C. (1995). External, internal and total work in human locomotion. *The Journal of Experimental Biology*, 198(Pt 2), 379–393.
- Willems, P. A., & Gosseye, T. P. (2013). Does an instrumented treadmill correctly measure the ground reaction forces? *Biology Open*, 2(12), 1421–1424. <https://doi.org/10.1242/bio.20136379>

Appendices

Figure S1. Effect of age on the bouncing mechanism of running.

Comparison of the spatiotemporal parameters of the running steps of older (27.6 y—dark grey bars) and younger (16.06 y—light grey bars) recreational runners [redrawn from (Legramandi et al., 2013; Schepens et al., 1998)]. Those ages were selected to match the age of the SOC and SWI groups. *Left*—Ratio between the duration of the deceleration (t_{brake}) and acceleration (t_{push}) phases of the COM across different running speeds. *Right*—Ratio between the effective contact (t_{ce}) and the effective aerial (t_{ae}) time across different running speeds. In each plot, the bars represent the mean. The absence of difference between groups suggests that the age does not affect the results of the present study.