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RESEARCH ARTICLE

Short- and long-term effects of altered point of ground reaction force application on human running energetics

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ABSTRACT

The current study investigates the effect of altering the point of force application (PFA) from the rearfoot towards the fore of the foot on the metabolic energy consumption and the influence of transitioning to this technique over a short or a longer timeframe. The participants were randomly assigned into two experimental and one control group: a short-term intervention group (STI, $N=17$; two training sessions), a long-term intervention group (LTI, $N=10$; 14-week gradual transition) and a control group (CG, $N=11$). Data were collected at two running velocities (2.5 and 3.0 m s^{-1}). The cost coefficient (i.e. energy required per unit of vertical ground reaction force; J N^{-1}) decreased ($P<0.001$) after both interventions due to a more anterior PFA during running (STI: 12%, LTI: 11%), but led to a higher ($P<0.001$) rate of force generation (STI: 17%, LTI: 15.2%). Dynamic stability of running showed a significant ($P<0.001$) decrease in the STI (2.1%), but no differences ($P=0.673$) in the LTI. The rate of metabolic energy consumption increased in the STI ($P=0.038$), but remained unchanged in the LTI ($P=0.660$). The CG had no changes. These results demonstrate that the cost coefficient was successfully decreased following an alteration in the running technique towards a more anterior PFA. However, the energy consumption remained unchanged because of a simultaneous increase in rate of force generation due to a decreased contact time per step. The increased instability found during the short-term intervention and its neutralization after the long-term intervention indicates a role of motor control errors in the economy of running after acute alterations in habitual running execution.

KEY WORDS: Lyapunov exponents, Nonlinear dynamics, Metabolic cost of locomotion, Running economy, Feedback training, Effective mechanical advantage

INTRODUCTION

Endurance running performance depends on a complex interplay between maximal oxygen uptake, the ability to sustain a high percentage of this uptake for long periods of time and the ability to move economically (Daniels et al., 1978; Lucia et al., 2006; Foster and Lucia, 2007; Fletcher and MacIntosh, 2017). Running economy, which is defined as the rate of oxygen consumption per unit body mass when running at a constant velocity (Daniels et al., 1978; Williams and Cavanagh, 1987) or as energy cost of running

expressed as the metabolic energy cost per body mass and per distance traveled (di Prampero et al., 1986; Margaria et al., 1963), has been regularly accepted to highly determine endurance running performance (Conley and Krahenbuhl, 1980; Daniels and Daniels, 1992; Joyner, 1991). Although numerous studies (Barnes and Kilding, 2015; Bonacci et al., 2009; Fletcher and MacIntosh, 2017; Moore et al., 2012; Nummela et al., 2007; Williams and Cavanagh, 1987) tried to identify the physiological and biomechanical factors that affect the energy cost of running, only a few employed interventional designs to directly improve the energy cost of running (Lake and Cavanagh, 1996; Moore et al., 2012; Albracht and Arampatzis, 2013; Clansey et al., 2014; Craighead et al., 2014).

It is reported that a higher Achilles tendon stiffness and a higher strength of the plantar flexor muscles are important properties of the human system affecting the energy cost of running (Arampatzis et al., 2006; Fletcher et al., 2010). Subsequent interventions based upon these observations found that a training protocol that increased the Achilles tendon stiffness and the muscle strength of the plantar flexors led to improvements in the energy cost of running of approximately 4% (Albracht and Arampatzis, 2013). Further, it has been suggested that the training-induced improvement in running economy might originate from a change of the effective mechanical advantages [EMA; i.e. the ratio of the muscle moment arm to the moment arm of the ground reaction force (Biewener, 1989)] within the lower limb (i.e. smaller EMA for the ankle and greater EMA for the knee joint) (Albracht and Arampatzis, 2013). Compared to the knee extensor muscles, the human plantar flexor muscles have shorter fascicles and are metabolically less costly than long-fibred muscles in generating the same force (i.e. lower active muscle volume for the production of the same muscle force) (Biewener and Daley, 2007). Therefore, an alteration of the EMA within the lower limb would initiate a redistribution of the muscular output within the lower extremities and might explain the observed improvement in energy cost of running (Albracht and Arampatzis, 2013). However, this hypothesis has not been investigated experimentally to date. From a biomechanical point of view, a shift of the point of ground reaction force application (PFA) during running from the rearfoot towards the fore of the foot would result in a longer moment arm of the ground reaction force at the ankle joint and in a shorter moment arm of the ground reaction force at the knee joint. Such a change would imply a smaller EMA for the ankle but a greater EMA for the knee joint.

Among numerous mammals, including humans, there is evidence that the rate of metabolic energy consumption of running is proportional to the rate of force applied to the ground (Kram, 2000; Kram and Taylor, 1990). Kram and Taylor (1990) found a nearly constant cost coefficient (energy required per unit force) across different animals and running speeds, and tested the 'cost of generating force' hypothesis (i.e. the cost of running is primarily determined by the cost of supporting mass and by the time course of force application). According to the concept formulated from

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List of abbreviations

CG	control group
d	effect size
EMA	effective mechanical advantage
FFS	forefoot strike pattern
FSP	foot strike pattern
LTI	long-term exercise intervention group
MFS	midfoot strike pattern
MLE	maximum Lyapunov exponents
PFA	point of ground reaction force application
RER	respiratory exchange ratio
RFS	rearfoot strike pattern
STI	short-term intervention group

Kram and Taylor (1990), the rate of metabolic energy consumption can be determined as the product of a constant factor (cost coefficient) and the rate of force applied to the ground, defined as the average vertical force exerted to the ground divided by the contact time. It should be mentioned that, although this calculation does not mathematically represent the actual rate of force applied to the ground (mathematically calculated as the first derivative of the ground reaction force over time), it is often used in the literature (Kram and Taylor, 1990; Roberts et al., 1998a,b; Wright and Weyand, 2001; Griffin et al., 2003; Karamanidis and Arampatzis, 2005; Vernillo et al., 2015) and we therefore used this term in the current study. We argue that a redistribution of the muscular output within the lower limb during human running towards greater EMA at the knee joint and lower EMA at the ankle joint could decrease the cost coefficient. This is due to the less costly force generation of the plantar flexor muscles compared to the knee extensor muscles, thus affecting the rate of metabolic energy consumption. In the present study, we investigated the effects of a feedback-directed alteration of the PFA towards the fore of the foot on the cost coefficient during running.

Transition towards a more anterior PFA results in several biomechanical adjustments during running (Biewener, 2016; Biewener and Daley, 2007; Williams et al., 2000). Employing and learning a novel locomotion strategy involves the central nervous system and can challenge the neuromuscular system (Wise and Willingham, 2009; Wolpert et al., 2011). Altered neuromechanical function during acute transition between running conditions can yield control errors and instabilities during running (Ekizos et al., 2017; Kelly et al., 2018). However, dynamic stability is required for effective and safe locomotion (Massion, 1992; Patla, 2003), whereas accurate neuromuscular control constitutes a determining factor of running performance (Bonacci et al., 2009). Lyapunov's theory of dynamic stability assesses the sensitivity of a mechanical system to small perturbations (Ihlen et al., 2017; Lyapunov, 1992) and is commonly adopted as a criterion for the occurrence of control errors during locomotion (Dingwell and Cusumano, 2000; Bruijn et al., 2013; Terrier and Reynard, 2014; Terrier and Dériaz, 2013; Reynard et al., 2014; Kao et al., 2014). Alterations to the self-selected running strategy, such as an intentional shift towards a more anterior PFA, may introduce control errors to the system, especially in the learning phase. These control errors when transitioning from one running strategy to another could play an important role on the energy cost of running. However, long-term training can enhance the processing of information and execution of locomotion (Bohm et al., 2015; Shadmehr et al., 2010; Wolpert and Miall, 1996), through spatial, temporal and functional adjustments of movements (Wolpert and Flanagan, 2001; Wise and Willingham, 2009; Wolpert et al., 2011), amending such control errors.

The objective of the present study was to understand the effects of an acute and a gradual change in the PFA towards the fore of the foot during running on the rate of metabolic energy consumption. Based on previous works regarding the EMA (Biewener, 1989; Biewener et al., 2004) and energetics of running (Kram, 2000; Kram and Taylor, 1990; Roberts et al., 1998b), we hypothesized that this shift would decrease the cost coefficient and lead to an improvement in the running economy. Further, our second hypothesis was that the execution of a novel running strategy could induce instabilities and negatively affect the metabolic energy consumption, and these could be alleviated by a long-term intervention training. The ability of our participants to perform the new technique was ensured through a custom-made software with feedback information. We measured steady-state oxygen consumption to calculate the energy cost of running, calculated the local dynamic stability as a measure of control errors, and measured biomechanical parameters to determine the mechanisms governing the transition.

MATERIALS AND METHODS
Experimental protocol
The current study involved 52 runners (>10 km week^{-1} and two running sessions week^{-1}) who gave informed consent to the study's procedures. In the study, only runners who employed a habitually rearfoot strike (RFS) were included. To select them, all participants ran in their preferred velocity for 2 min on a pressure-plate-equipped treadmill with their habitual running technique (120 Hz acquisition frequency; FDM-THM-S, zebris Medical GmbH, Germany). We identified the RFS runners using the algorithm of Santuz et al. (2016). The foot strike pattern (FSP) was numerically quantified through the strike index (i.e. the distance from the heel to the center of pressure at first impact, relative to total foot length) based on the recorded foot pressure distribution using a validated algorithm (Santuz et al., 2016). An RFS was considered one that provided a strike index lower than 1/3 of the total foot length, a midfoot strike (MFS) one that provided values between 1/3 and 2/3, and a forefoot strike (FFS) one with values above 2/3 of the total foot length (Cavanagh and Lafortune, 1980).

The participants were randomly divided into three groups: a short-term intervention group (STI: N=18; 5 female), a long-term exercise intervention group (LTI: N=17; 9 female) and a control group (CG: N=17; 12 female). Identical measurements were conducted before and after the interventions in all groups. All groups performed an identical pre- and post-measurement. The measurement procedure consisted of the participants running on a pressure-plate-equipped treadmill. Our participants ran at two different fixed velocities: 2.5 and 3.0 m s^{-1} after a short acclimatization period (1 min), and for 6 min at each velocity. No visual, verbal or other feedback was provided during the measurements. Further, no instructions or introduction to the specific target of the study were given to the participants prior to the pre-measurements. None of the participants had any musculoskeletal or neuromuscular impairments at the time of the measurements or during the 6 months prior to them. The study was conducted in accordance to the university ethical guidelines (Humboldt-Universität zu Berlin). All participants gave informed consent and the approval of the local ethics committee (Humboldt-Universität zu Berlin) was obtained.

With the STI, we investigated the effect of acutely transitioning from an RFS into running employing an MFS. Following the baseline measurements, the participants were introduced to the aim of the study and performed a short-term feedback-enhanced intervention (i.e. two 30 min sessions separated by 2 days). A session consisted of two parts. Firstly, the participants executed a

short run on the treadmill trying to achieve an MFS running. Afterwards, they visually inspected their foot pressure imprints through a proprietary pressure plate software (WinFDM-T v2.5.1, zebris Medical GmbH, Germany). They were then presented with the numerical value of their strike index and its comparison to previous trials, the force development during contact as well as their average pressure distribution of all steps at the first contact of the foot. A typical visual output from the custom-developed software is presented in Fig. 1. Secondly, they received verbal feedback from an experienced researcher. The researcher customized the verbal instructions to each participant with focus on: shifting their body mass forward and concentrating on the movement of the ankle joint. Simple physical exercises (i.e. lean forward and run against a rope; lean forward against a rope and sudden rope release) were introduced if necessary. This procedure was repeated as appropriate with a focus on the visual cues by the proprietary and the custom software. To assure competence and ability to execute the new running technique, the participants performed two similar 30 min sessions on the treadmill with feedback information regarding FSP. Post-measurements were conducted 4 days after the pre-measurements, with prior instruction to maintain the new MFS running technique but without any feedback information during the whole period of the 6 min per velocity. One participant was unable to maintain the new pattern for the whole period of 6 min during the post-measurements and was excluded from our results (STI: $N=17$; 4 female).

The aim of the LTI was to investigate the effect of a long-term intervention targeting the transitioning from an RFS into running employing an MFS. The long-term feedback-based intervention lasted 14 weeks in total and consisted of three parts. First, the participants were instructed to gradually exchange part of their training volume on their normal FSP with equal parts of MFS running. The amount was individually tailored to the participants who consulted with an experienced researcher. Second, they performed three times per week a session, which lasted ~30 min each, in addition to their normal training volume. The training included a set of exercises aiming to prepare and aid the transition into running with an MFS. The exercises focused at the lower extremities to prepare them for the added loading (i.e. step up with high knee, lunges landing on midfoot), on whole-body stability in order to support the transition to a more forward leaning pose and on running technique with emphasis on MFS running simulation exercises. Third, each week participants performed a specialized session (~30 min) in our lab. In this session, they received extensive verbal and visual cues on their running technique as we described in the training of the STI. Six participants dropped out due to time restrictions in performing the intervention and one due to injury, unrelated to the intervention program. Post-measurements were conducted 1 week after the completion of the exercise program in the remaining participants ($N=10$; 3 female). The participants were instructed prior to the post-measurements to keep the new MFS
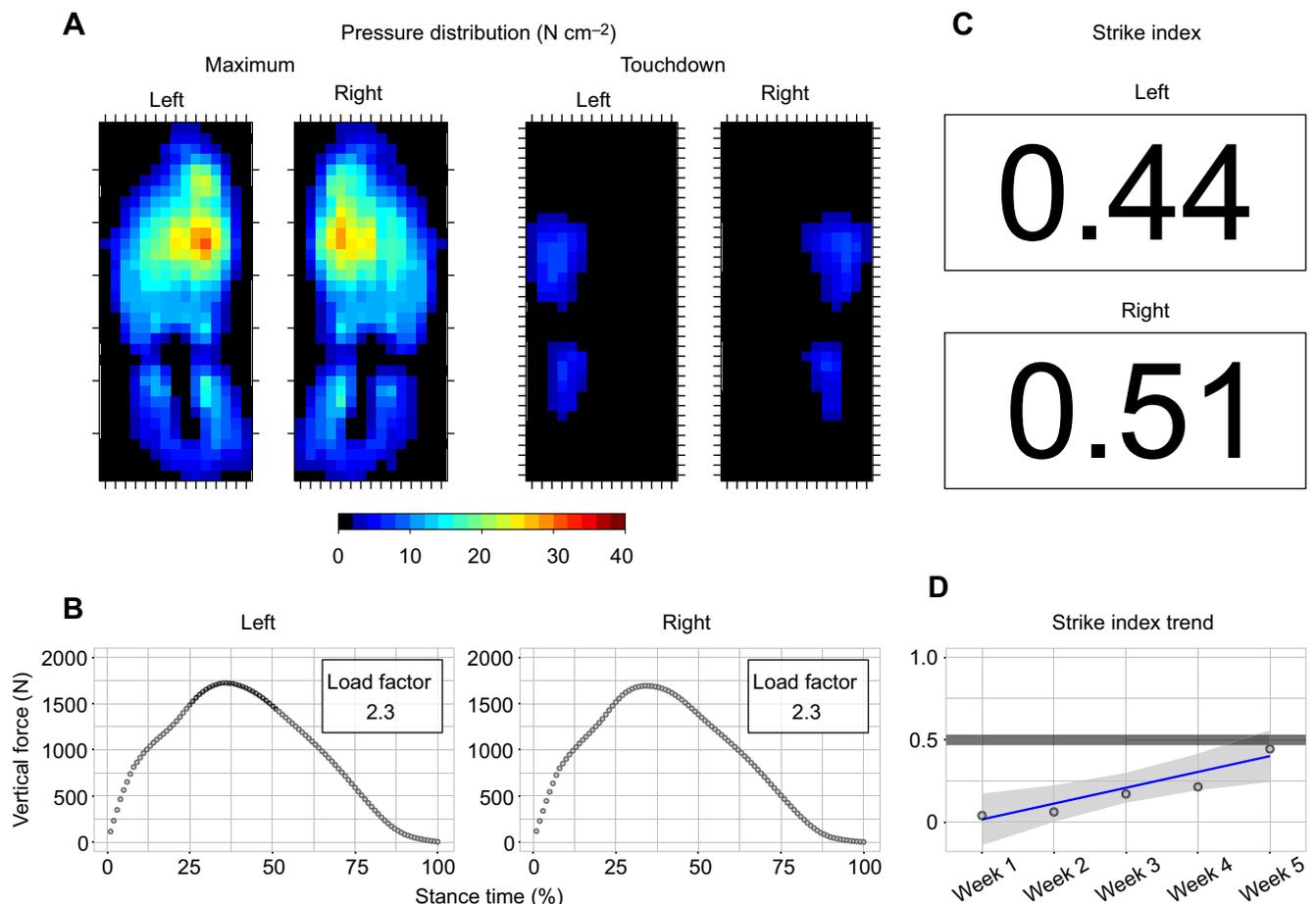

Fig. 1. Visual output from the custom-developed software. The figure is an example depicting the average values over all steps: pressure distribution at the timings of maximum pressure and at first contact (A), the numerical force output during contact time (B) and the strike index (C). The current strike index was also visualized in comparison to that of any previous trials (D); the gray horizontal line shows the targeted value of 0.5.

technique without any feedback information during the actual measurements for the whole 6 min in both velocities. Participants in the CG were instructed to maintain their training habits unaltered until the post-measurements, which took place 15 weeks after the baseline. Six participants dropped out due to time restrictions and did not participate in the post-measurements (N=11; 7 female).

Experimental setup
Two trials of 120 s were captured at each velocity. Both trials were captured amid the 6 min run on the treadmill. From the raw plantar pressure distribution values over time, we extracted: cadence, contact and flight time, average force per step, ground reaction forces and FSPs. To exclude any time-dependent effect of the pressure plate sensors on the LTI and CG, we measured overground ground reaction forces on a force plate (AMTI BP400600-2000, Watertown, USA) on a separate session and used these force values for subsequent analysis. We ensured that participants achieved exactly the same velocities (2.5 m s^{-1} and 3.0 m s^{-1}) as during treadmill running with the use of light barriers (velocity tolerance level was set to 0.05 m s^{-1}). The average of three trials at each speed was used for subsequent calculations. All participants contacted the plate with the same foot (i.e. the right foot) in all trials.

During the treadmill trials, four high-speed video cameras (Flare 4M180-CCL, IO Industries Inc., Canada) operating at 170 Hz captured four reflective 14 mm markers positioned on the spine (Ekizos et al., 2017). Namely, the second, seventh, tenth, thoracic and the second lumbar vertebrae were recorded. The automated tracking was performed using dedicated software (Simi Motion 9.2.0, Simi Reality Motion Systems GmbH, Germany). The videos were synchronized with the pressure plate using an analog signal triggered by the video capturing software (Simi Grab 2.1.1, Simi Reality Motion Systems GmbH, Germany). A fourth order Butterworth 20 Hz low-pass filter was applied to the registered coordinates, maintaining the maximum dynamics of the system (Sinclair et al., 2013).

Local dynamic stability
Local dynamic stability was calculated through the maximum Lyapunov exponents (MLE). We calculated the MLE on the vertical axis of the clustered coordinate data of the four markers registered on the spine (i.e. on the averaged coordinates of the four markers) according to the procedure used by a previous study (Ekizos et al., 2017). In short, after identifying the maximum common steps of all participants in each group and all trials in the duration of 120 s, we extracted the corresponding data segment for each trial. This segment was then normalized to a uniform data length of ~18,500 data points. We reconstructed the state space of the input one dimensional (1D) series through delay-coordinate embedding (Packard et al., 1980) as follows:

$$\mathbf{S(t)} = \{z(t), z(t+\tau), \ldots, z[t+(m-1)\tau]\}, \qquad (1)$$

with $\mathbf{S(t)}$ being the m-dimensional reconstructed state vector, $z(t)$ the input 1D coordinate series, τ the time delay and m the embedding dimension. Time delays were selected based on the first minimum of the average mutual information curve (Fraser and Swinney, 1986) and number of embedding dimensions through a global false nearest neighbors analysis (Kennel et al., 1992), with a threshold of one per thousand data points. Individually selected time delays were chosen by averaging the outcome delays of all individual time series for each of the participants (Ekizos et al., 2017). For our data, m=3 was sufficient for all subjects, while τ

ranged from 19 to 24 frames (~0.33 of average step). We then calculated the average divergence of each point's trajectory to its closest, employing the Rosenstein algorithm (Rosenstein et al., 1994). The MLE was calculated from the slopes of linear fits to the resulting average divergence curves on the frames equal to one step. The smaller the MLE, the more stably the system responds locally to small variations or perturbations.

Metabolic cost of running
Oxygen consumption (ml min^{-1}) during running was measured at both velocities (2.5 and 3.0 m s^{-1}) using an indirect calorimetry system (Metalyzer 3B, CORTEX Biophysik GmbH, Germany) with an acquisition frequency of ~0.5 Hz. Oxygen uptake was measured for 6 min, during which the researchers visually inspected and confirmed the respiratory exchange ratio (RER) to be <1.0. The last 3 min of each trial were averaged to calculate the oxygen consumption of each individual at each velocity. Recent reports have called attention to the significance of the transformation of the rate of oxygen consumption in its energy equivalent (Fletcher et al., 2009; Kipp et al., 2018). We therefore used the RER (i.e. 5.1573×RER+15.969 J ml^{-1} O$_2$) to convert measurements of oxygen consumption to rate of metabolic energy consumption. Further, we determined the cost coefficient (c) according to Kram and Taylor (1990). Kram and Taylor (1990) found a constant cost coefficient (energy required for a unit force; J N^{-1}) across different animals and running velocities, and evidenced that the rate of metabolic energy consumption ($\dot{E}$; W) of a running animal is proportional to the rate of force application on the ground (F_{rate}; N s^{-1}). Therefore, the cost coefficient can be assessed by the following equations:

$$\dot{E} = c \cdot F_{rate} \Rightarrow c = \frac{\dot{E}}{F_{rate}}. \qquad (2)$$

The rate of force generation was the quotient of the division of the average vertical ground reaction forces by the duration of the ground contact (Kram and Taylor, 1990; Roberts et al., 1998b):

$$F_{rate} = \frac{\bar{F}_{vertical}}{t_{contact}}. \qquad (3)$$

The oxygen consumption was normalized to body mass, while the rate of metabolic energy consumption was not. All raw data were post-processed using custom algorithms (MATLAB 2014b, MathWorks Inc., USA; R version 3.1.2, R Core Team, Vienna, Austria; http://www.R-project.org/).

Statistics
The effects of the short intervention (two sessions) have been investigated with a repeated measures two-way ANOVA, with pre- and post-measurements and velocity as within-subjects factors. The effects of the long intervention (14 weeks) were tested using a repeated measures mixed-design ANOVA with pre- and post-measurements and velocity as within-subjects factors, and group (LTI and CG) as between-subject factor (SPSS v.24, International Business Machines Corp., USA). A Bonferroni-corrected post hoc analysis was conducted in the case of a significant time effect or interaction of the factors time and intervention. To compare the anthropometric data between groups, we used a one-way ANOVA. The level of significance was set to α=0.05. Furthermore, to estimate the strength of potential alterations of the investigated parameters following the exercise interventions, the effect size (d) was calculated. Values of d<0.2 indicate small effect sizes,

Table 1. Strike index, contact time, flight time, cadence and oxygen consumption of the short-term intervention group (STI, N=17) over the two velocities

Parameter	2.5 m s⁻¹			3.0 m s⁻¹		
	Pre	Post	d	Pre	Post	d
Strike index (dimensionless)‡	0.09±0.05	0.53±0.12	4.84	0.08±0.05	0.51±0.16	3.65
Contact time (ms)‡	309±30	289±26	0.72	279±23	262±18	0.82
Flight time (ms)‡	64±27	85±23	0.83	84±22	99±20	0.73
Cadence (steps min⁻¹)	161.7±7.8	161.2±8.6	0.06	165.7±9.5	166.3±8.8	0.06
Oxygen consumption (ml min⁻¹ kg⁻¹)‡	32.5±4.6	33.5±5.6	0.20	38.0±4.8	38.9±5.7	0.17

Values are means±s.d. ‡Statistically significant time effect ($P<0.05$). d, Cohen's effect size.

$0.2 \leq d < 0.8$ indicate medium sizes and $d \geq 0.8$ indicate large effect sizes (Cohen, 1988). To examine the relationship between investigated parameters (i.e. rate of metabolic energy consumption and rate of force generation), the Pearson correlation coefficient was used.

RESULTS
Anthropometric data for the STI ($N=17$; age: 31±4 years; height: 178±9 cm; body mass: 73±12 kg), LTI ($N=10$; age: 33±5 years; height: 178±8 cm; body mass: 71±8 kg) and CG ($N=11$; age: 31± 3 years; height: 175±9 cm; body mass: 69±10 kg) presented no significant differences (age: $P=0.431$, height: $P=0.611$, body mass: $P=0.729$). Considering the baseline measurements (i.e. only the values obtained as pre-measurements) and including both investigated velocities and all three groups, the rate of metabolic energy consumption showed a high correlation with the rate of force generation ($r=0.673$, $P<0.001$, Fig. 2).

Short-term intervention
After the two 30 min training sessions, all the participants of the STI were able to change their FSP from an RFS to an MFS. The average strike index increased significantly ($P<0.001$) in the post-measurements at both investigated velocities (Table 1). The contact time presented significantly lower values ($P<0.001$), while the flight time significantly increased ($P<0.001$), in the post- compared to the pre-measurements (Table 1). Cadence remained unchanged before and after the training sessions ($P=0.961$, Table 1). The MLE values increased significantly ($P<0.001$) after the training sessions at both velocities (Fig. 3). The cost coefficient decreased significantly

Fig. 2. Relationship between the rate of metabolic energy consumption ($\dot{E}$) and rate of force application on the ground (F_{rate}) for all investigated participants and running velocities. $N=76$.

($P<0.001$) compared with the baseline measurements, where the rate of force applied to the ground increased ($P<0.001$) after the intervention (Fig. 3). The oxygen consumption and the rate of metabolic energy consumption increased significantly ($P=0.010$, Table 1 and $P=0.038$, Fig. 3, respectively) after the training sessions.

Long-term intervention
All the participants of the LTI changed their FSP from an RFS to an MFS after the long-term (14 weeks) intervention. By contrast, no participant of the CG changed their original FSP, with all of them maintaining an RFS before and after 14 weeks. For the strike index there was a time by group interaction ($P<0.001$). There was a significant ($P<0.001$) increase in the strike index for the LTI, but not in the CG ($P=0.277$, Table 2). Regarding contact and flight time there was a time by group interaction for both parameters ($P<0.001$ and $P=0.003$, respectively). After the intervention program, the LTI presented significantly lower contact time and significantly increased flight time (both $P<0.001$). No statistically significant differences (contact time: $P=0.292$, flight time: $P=0.561$) were observed in the CG (Table 2). Cadence and MLE did not show any significant time effect ($P=0.817$ and $P=0.673$, respectively) after the 14 weeks (Table 2, Fig. 4).

The cost coefficient exhibited a time by group interaction ($P=0.045$). For the LTI the cost coefficient decreased significantly ($P<0.001$) compared with the pre-measurements, with no significant ($P=0.416$) changes observed in the CG (Fig. 4). We also found a time by group interaction ($P<0.001$) for the rate of force generation. The rate of force generation was significantly higher in the post-measurements ($P<0.001$) in the LTI. The CG did not show any statistically significant ($P=0.141$) changes after the 14 weeks (Fig. 4). The oxygen consumption (Table 2) and the rate of metabolic energy consumption (Fig. 4) did not change in the LTI or the CG ($P=0.599$ and $P=0.660$) after the 14 weeks.

DISCUSSION
The present study investigated the effect of an acute and a gradual change in the PFA towards the fore of the foot on the rate of metabolic energy consumption during running following a short-term (two sessions within 1 week) and a long-term (14 weeks) intervention. After completing the short- or long-term interventions, both the STI and the LTI changed to a more forward PFA, which was evident by the increase in the strike index. The modified strike index resulted, indeed, in the decrease of the cost coefficient in both exercised groups during running. However, despite the reduction in the cost coefficient, the rate of metabolic energy consumption increased in the STI and remained unchanged in the LTI. Therefore, our first hypothesis (i.e. a shift towards a more forward PFA would decrease the cost coefficient and lead to an improvement in the running economy) has been rejected. By contrast, the control errors induced by the acute change to the new running technique were
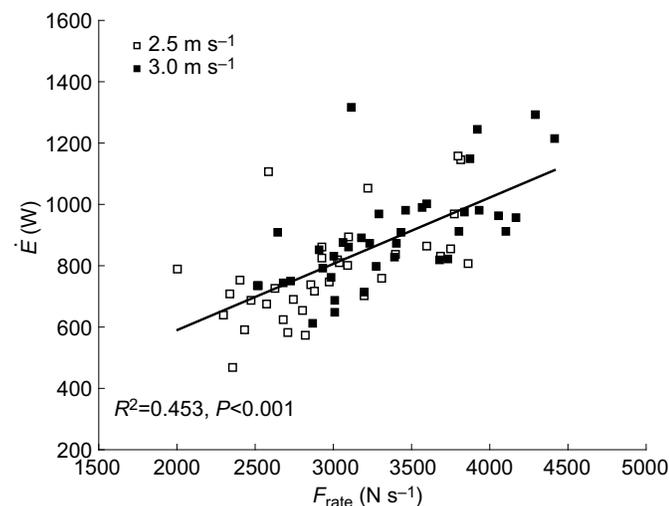
Table 2. Strike index, contact time, flight time, cadence and oxygen consumption of the long-term intervention and the control group over the two velocities

| Parameter | Long-term intervention group (N=10) | | | | | | Control group (N=11) | | | | | |
| | 2.5 m s⁻¹ | | | 3.0 m s⁻¹ | | | 2.5 m s⁻¹ | | | 3.0 m s⁻¹ | | |
	Pre	Post	d	Pre	Post	d	Pre	Post	d	Pre	Post	d
Strike index (dimensionless)‡,#	0.09±0.03	0.51±0.16*	3.60	0.08±0.02	0.48±0.20*	2.82	0.05±0.02	0.05±0.03	0.14	0.05±0.01	0.05±0.01	0.24
Contact time (ms)‡,#	300±21	277±17*	1.19	277±17	254±15*	1.41	330±18	328±25	0.06	295±11	292±16	0.19
Flight time (ms)‡,#	80±19	102±15*	1.30	90±17	110±17*	1.15	48±29	50±31	0.06	73±24	74±28	0.04
Cadence (steps min⁻¹)	158.7±11.7	158.4±7.7	0.03	164.4±11.8	165.5±10.1	0.10	159.5±10.6	159.0±8.6	0.05	163.7±11.4	164.3±10.3	0.05
Oxygen consumption (ml min⁻¹ kg⁻¹)	34.0±2.6	34.7±1.5	0.29	38.3±2.4	39.1±3.5	0.28	31.2±4.0	31.1±2.4	0.03	36.9±3.7	36.8±2.8	0.03

Values are means±s.d. Outcome parameters before (pre) and after (post) the intervention for the two study groups. d, Cohen's effect size.
‡Statistically significant time effect ($P<0.05$).
#Statistically significant time by group interaction ($P<0.05$).
*Statistically significant differences (post hoc analysis) between pre- and post-intervention values ($P<0.05$).

alleviated by the long-term intervention, confirming our second hypothesis (i.e. a novel running strategy could induce instabilities, negatively affecting the energy cost of running and their alleviation by a long-term intervention training).

Although the cost coefficient of running in humans and other mammals is nearly constant across different velocities (Kram, 2000; Kram and Taylor, 1990), it is well accepted that the muscle EMA may affect the cost coefficient of locomotion in humans (Biewener
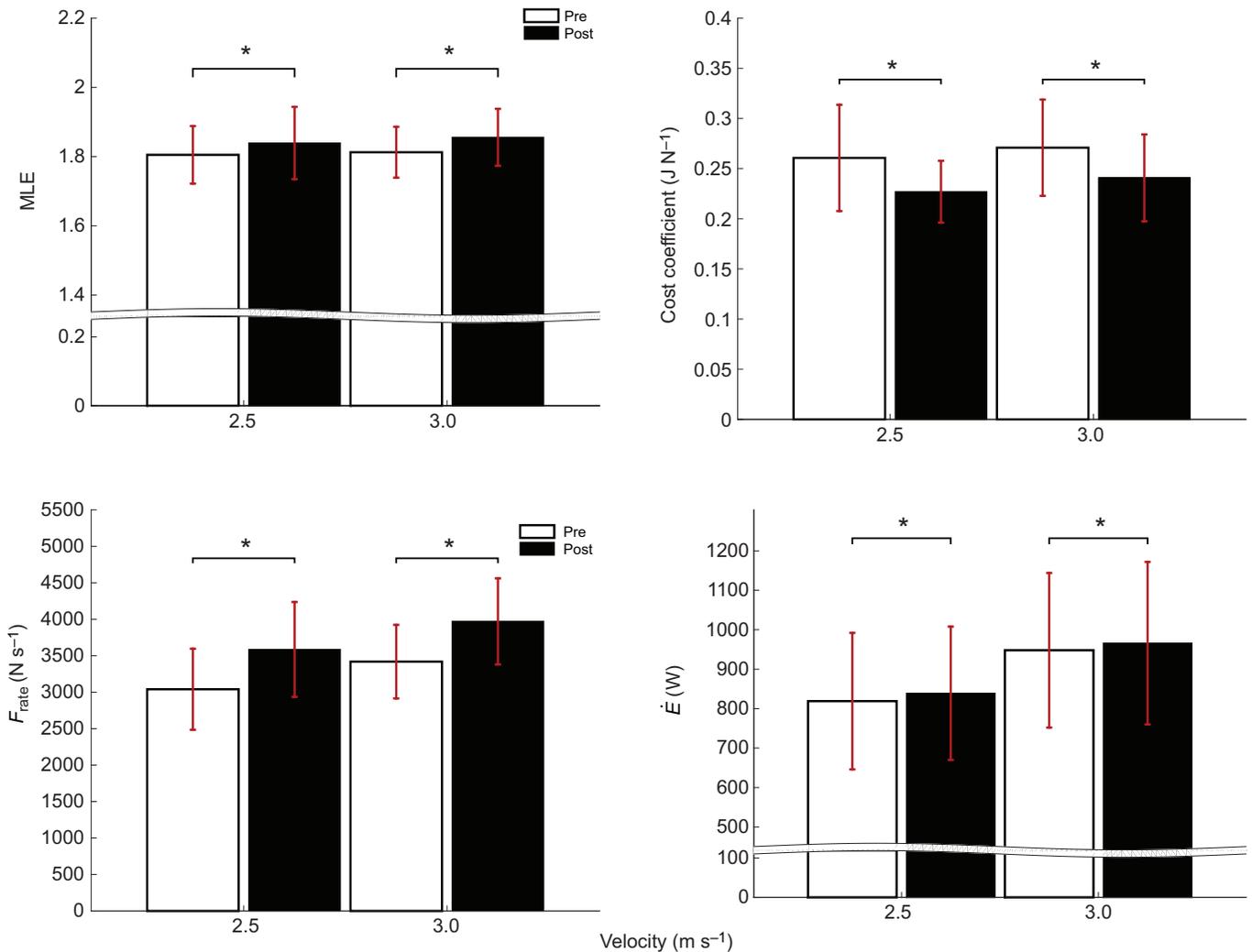

Fig. 3. The maximum Lyapunov exponents (MLE), cost coefficient, rate of force development (F_{rate}) and rate of metabolic energy consumption ($\dot{E}$) presented for the short-term intervention group (STI), during running at 2.5 and 3.0 m s⁻¹, before and after the short-term intervention. *Statistically significant differences (post hoc analysis) between pre- and post-intervention values ($P<0.05$). N=17.

et al., 2004) and animals (Biewener, 1990; Roberts et al., 1998a,b) due to resulting changes in the active muscle volume. Biewener et al. (2004) demonstrated that the increased energy cost of running compared to walking is due to the lower EMA of the knee extensor muscles in running. Roberts et al. (1998a,b) reported that the higher cost coefficient in birds compared to humans and quadrupedal mammals resulted from the greater ratio of muscle fiber length to muscle EMA. With the anterior shift of the PFA, we intended a modification of the EMA within the lower extremities (i.e. smaller EMA for the ankle and greater EMA for the knee joint) and in this way a metabolically less costly force generation. There is indeed evidence in the literature for a redistribution of the muscular output in the lower extremities when runners move the PFA towards the fore of the foot (Davis et al., 2017; Hamill and Gruber, 2017). A greater demand on the plantar flexor muscles and a lower demand of the knee extensor muscles is observed in runners who employ an FFS compared to runners who employ an RFS (Kulmala et al., 2013; Stearne et al., 2014; Kuhman et al., 2016). Compared to the knee extensor muscles, the human plantar flexor muscles have shorter fascicles. Shorter muscle fascicles decrease the ratio of

active muscle volume to muscle physiological cross-sectional area by a given muscle force generation because typically muscle force is proportional to the active physiological cross-sectional area (Haxton, 1944). This implies an energetic advantage for the plantar flexors and can affect the cost coefficient. Indeed, the decreased cost coefficient after the anterior shift of the PFA in both the STI and LTI suggests lower metabolic energy consumption per unit force in the post-measurements. Previous studies provided evidence that the energy cost of running is primarily dependent on the cost of producing force in order to support the body mass (Kram and Taylor, 1990; Taylor, 1985; Taylor et al., 1980). It has been argued that the energy used by a unit volume of active muscle in a running animal is inversely proportional to the time needed to produce force (Kram and Taylor, 1990), because faster muscle fibers, which are metabolically more expensive, have to be recruited (Alexander and Ker, 1990; Kram and Taylor, 1990; Rall, 1985).

In our study, the rate of force applied to the ground showed a high correlation to the rate of metabolic energy consumption during running, supporting previous observations that the cost of producing force to support the body mass depends on the contact time (Griffin
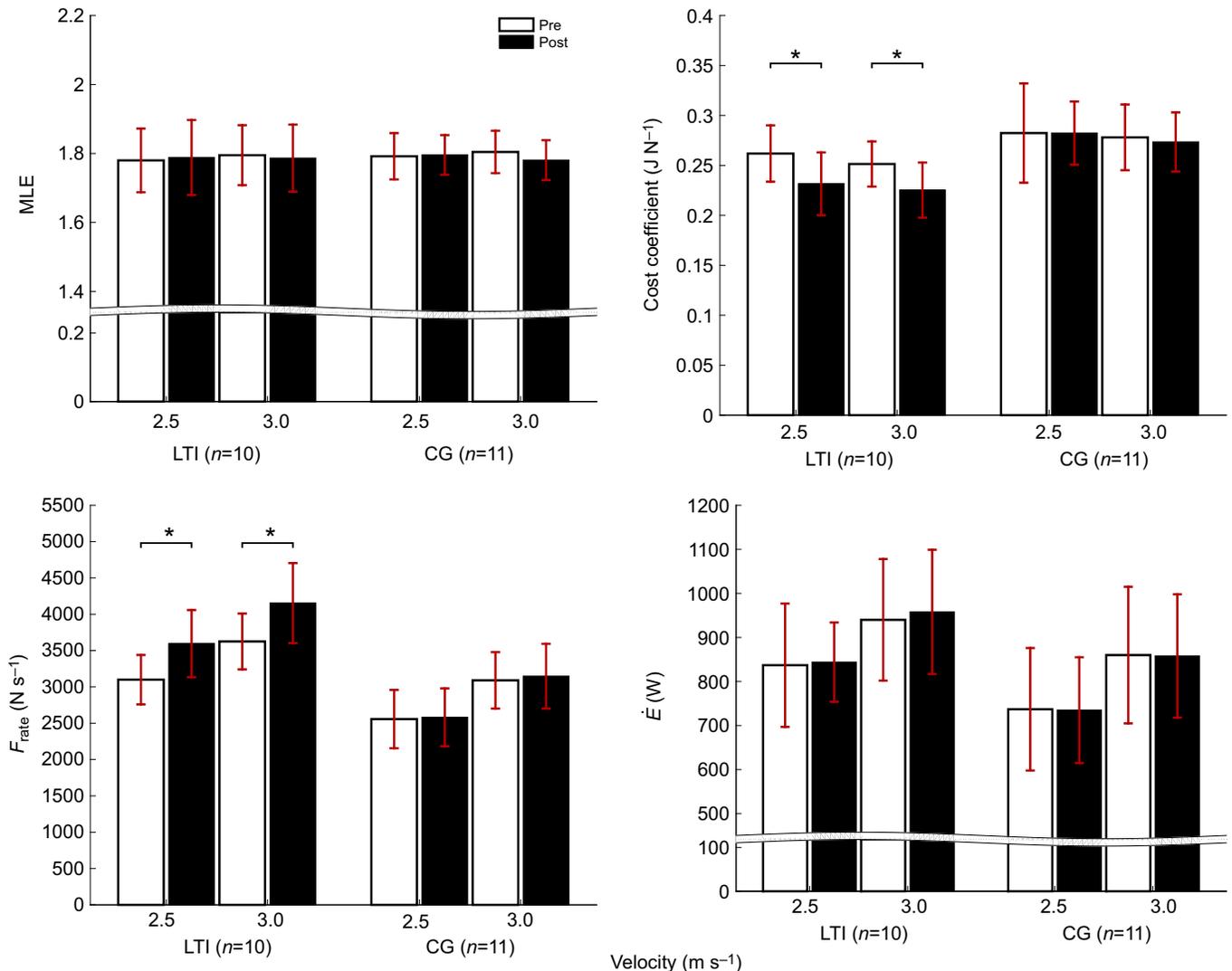

Fig. 4. The MLE, cost coefficient, rate of force development (F_{rate}) and rate of metabolic energy consumption ($\dot{E}$) presented for the long-term intervention group (LTI) and control group (CG), during running at 2.5 and 3.0 m s^{-1}, before and after the short-term intervention. *Statistically significant differences (*post hoc* analysis) between pre- and post-intervention values ($P<0.05$).

et al., 2003; Kram and Taylor, 1990; Roberts et al., 1998b; Wright and Weyand, 2001). Although cadence did not change in both groups, the anterior shift of the PFA led to shorter contact times and longer flight times while running. The shorter contact time at the same running velocity was the reason for the increased rate of force generation, which affects the rate of metabolic energy consumption. While running, the increased rate of force applied to the ground in the STI and the LTI means that both groups had to produce the necessary force to support body mass faster in each step and thus negatively affected the rate of metabolic energy consumption. Both interventions induced a decrease in the cost coefficient (STI: 12%, LTI: 11%) following an alteration in the running technique towards a more anterior PFA. However, this decrease did not produce a positive effect to the rate of the metabolic energy consumption, because of an increased rate of force generation (STI: 17%, LTI: 15.2%) due to a decreased contact time per step. The inversely proportional changes of these two factors (i.e. cost coefficient and rate of force applied to the ground), which influence the rate of metabolic energy consumption, explain the absence of improvements in the rate of metabolic energy consumption during running after the interventions. Similar reports and explanations have been provided by comparing the energy cost of locomotion between turkeys and dogs (Roberts et al., 1998a). Although dogs showed a lower cost coefficient compared to turkeys, the higher rate of force applied to the ground neutralized the advantage of the cost coefficient and resulted to similar energetic cost of locomotion in trotting dogs and running turkeys (Roberts et al., 1998a).

Furthermore, in the STI we found an increase in the rate of metabolic energy consumption of 2.7% after the shift of the PFA towards the fore of the foot (i.e. worsening of the energy cost of running) despite an improvement in the cost coefficient. In the STI, the MLE during running increased (2.1%) after the two-session exercise. The increased MLE corresponds to a more chaotic and unstable dynamical system (Bradley and Kantz, 2015; Kantz and Schreiber, 2004) and indicates control errors in the neuromuscular control of locomotion (Bruijn et al., 2013; Dingwell and Cusumano, 2000). Maintaining dynamic stability control is a prerequisite for successful execution of locomotion (Bohm et al., 2015; Patla, 2003; Winter, 1987). Learning new movements involves a number of interacting components, which include detection, processing and transmission of sensory signals to appropriate motor commands (Wolpert et al., 1998, 2011), and therefore errors in the motor control and learning may affect the energy cost of locomotion. On uneven surfaces where stability is challenged (Santuz et al., 2018), the rate of metabolic energy consumption is also increased (Voloshina and Ferris, 2015). Moreover, it has been suggested that 2% of the net energetic cost of running is attributed to maintaining stability in the lateral direction (Arellano and Kram, 2012). Studies on animals showed that animals often choose to optimize locomotion patterns to achieve increased stability, compromising energetically optimal mechanical work output and, thus, decreasing economy (Daley and Usherwood, 2010). We can argue that the decreased stability after two exercise sessions provides evidence of motor control errors during running and leads to an additional cause of the increased rate of metabolic energy consumption in the STI.

After 14 weeks of exercise in which we trained the PFA towards the anterior of the foot, the MLE showed no differences compared to the pre-intervention values, indicating no control errors compared to the habitual running technique. Combining the findings of the short- and long-term interventions we provide evidence that exercise-induced alteration of the habitual self-selected running technique

leads to short-term instabilities challenging the energy cost of running. However, the initial instabilities were overcome by continued training with the new running technique. Following recent paradigms of renormalization of motor control during skill acquisition (Makino et al., 2016; Wenger et al., 2017), our results exhibit that we altered the self-chosen habitual running technique into a new one, successfully negating the instabilities and ensuring a renormalization of the motor output. Acute changes in the running technique cannot yield immediate improvements in running economy and evidence the need for a gradual long-term intervention to overcome stability losses. Furthermore, as locomotion constitutes an emergent functional property (Biewener, 2016), we observe an interplay between different mechanisms that affect and can have counterbalancing effects on the energy cost of running. This could be the reason behind discrepancies in the literature, since some studies suggest no benefit from a change in a more forward PFA (Gruber et al., 2013; Ogueta-Alday et al., 2014), while others do suggest benefits (Di Michele and Merni, 2014). Based on the results of the current study, future interventions aiming to improve running economy could focus on changes in the PFA towards the fore of the foot during running, while maintaining similar contact times.

It has been shown that cost coefficients remain relatively constant across running velocities (Kram and Taylor, 1990; Hoyt et al., 1994). In our study, although the cost coefficient was changed after both short- and long-term intervention, it did not show any differences between the two investigated running velocities. Furthermore, the strong relationship between the rate of metabolic energy consumption and the rate of force application on the ground supported the formulated concept from Kram and Taylor (1990) that the cost of running is primarily determined by the cost of supporting mass and by the time course of force application. The assumption in this concept is that muscles are working at similar ranges of their force–velocity relationships at steady-state running speeds (Kram, 2000). Recently, studies that measured the fascicle length of the gastrocnemius medialis (Albracht and Arampatzis, 2013) and soleus (Lai et al., 2015) reported similar shortening velocity of the fascicles in both muscles during different running velocities, evidencing a similar force–velocity potential of these muscles in a range of running speeds. To what extent more proximal muscles, for example the knee extensors, show similar force–velocity potential by different running velocities remains to be seen in future research.

Conclusions

The present study found a decrease in the cost coefficient following an alteration in the running technique towards a more anterior PFA. However, the metabolic energy consumption remained unchanged after the intervention, due to a simultaneous increase in the rate of force generation which resulted from a decreased contact time per step. Our results indicate the existence of an additional mechanism that negatively affects the economy of running when the transition to an anterior PFA is acute. The increased instability during the acute transition and its neutralization after the long-term intervention provide evidence that motor control errors can have a role in the economy of running after acute alterations in habitual running execution.

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