

ORIGINAL ARTICLE

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Energy cost and running mechanics during a treadmill run to voluntary exhaustion in humans

Accepted: 15 September 1997

Abstract The aim of the present study was to examine the physiological and mechanical factors which may be concerned in the increase in energy cost during running in a fatigued state. A group of 15 trained triathletes ran on a treadmill at velocities corresponding to their personal records over 3000 m [mean 4.53 (SD 0.28) $\text{m} \cdot \text{s}^{-1}$] until they felt exhausted. The energy cost of running (C_R) was quantified from the net O_2 uptake and the elevation of blood lactate concentration. Gas exchange was measured over 1 min firstly during the 3rd–4th min and secondly during the last minute of the run. Blood samples were collected before and after the completion of the run. Mechanical changes of the centre of mass were quantified using a kinematic arm. A significant mean increase [6.9 (SD 3.5)%, $P < 0.001$] in C_R from a mean of 4.4 (SD 0.4) $\text{J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$ to a mean of 4.7 (SD 0.4) $\text{J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$ was observed. The increase in the O_2 demand of the respiratory muscles estimated from the increase in ventilation accounted for a considerable proportion [mean 25.2 (SD 10.4)%] of the increase in C_R . A mean increase [17.0 (SD 26.0)%, $P < 0.05$] in the mechanical cost (C_M) from a mean of 2.36 (SD 0.23) $\text{J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$ to a mean of 2.74 (SD 0.55) $\text{J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$ was also noted. A significant correlation was found between C_R and C_M in the non-fatigued state ($r = 0.68$, $P < 0.01$), but not in the fatigued state ($r = 0.25$, NS). Furthermore, no correlations were found between the changes (from non-fatigued to fatigued state) in C_R and the changes in C_M suggesting that the increase in C_R is not solely dependent on the external work done per unit of distance. Since step frequency decreased slightly in the fatigued state, the internal work would have tended to decrease slightly which would not be compatible with an increase in C_R . A stepwise regressions showed that the

changes in C_R were linked ($r = 0.77$, $P < 0.01$) to the changes in the variability of step frequency and in the variability of potential cost suggesting that a large proportion of the increase in C_R was due to an increase in the step variability. The underlying mechanisms of the relationship between C_R and step variability remains unclear.

Key words Running economy · Ventilation · Mechanical work · Step frequency · Step variability

Introduction

Several studies have been conducted to establish possible relationships between energy cost of running (C_R) and running mechanics (Martin et al. 1993; Shorten et al. 1981; Williams 1985, 1990; Williams and Cavanagh 1987). However, it has seemed very difficult to find consistent relationships between C_R and biomechanical variables (Morgan et al. 1990; Williams 1985). For instance, the differences in running economy between good and elite runners that have been reported (Cavanagh et al. 1977) could not be directly attributed to differences in the mechanical parameters measured.

In the fatigued state, an increase in C_R has been found when compared to the non-fatigued state (e.g. Brueckner et al. 1991). It has been shown that during heavy exercise, oxygen uptake ($\dot{V}\text{O}_2$) does not achieve a steady state but continues to rise for several minutes until exercise is ended, or exhaustion ensues (Barstow and Molé 1991; Poole et al. 1991). The mechanisms of this slow component of $\dot{V}\text{O}_2$ kinetics (i.e. increase in C_R) are still under discussion. One of the proposed explanations has been a rise in energy demand of the respiratory muscles due to an hyperventilation in the fatigued state (Poole et al. 1991). However, to the best of our knowledge no quantitative information has been presented. It also seems reasonable to assume that an increase in energy expenditure in the fatigued state may be due in part to an increase in the mechanical work per

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unit of distance. However, no relationship between C_R and the mechanical cost of running (C_M) has been demonstrated in the fatigued state.

An increase in C_R could also be explained by a reduced ability to store and mechanical energy in running. In the fatigued state, a change in muscle stiffness characteristics (Nicol et al. 1996) and, hence a decline in the amount of mechanical energy stored and has been hypothesised by Komi et al. (1986). This hypothesis has been supported by a greater decline in force after the initial peak force of the impact (Komi et al. 1986; Nicol et al. 1991) and an increase in stride length, support to flight time ratio (Buckalew et al. 1985) during or after exhausting running compared to the non-fatigued state. An inaccurate control of step frequency in the fatigued state could also result in a reduced energy recoil and in an increased C_R . In the non-fatigued state, the existence of an optimal step frequency in terms of energy cost has been shown (Cavagna et al. 1991; Kaneko 1987; Taylor 1985). To summarise, the increase in C_R with fatigue could be due to the combined action of both physiological and mechanical parameters.

Recently, a kinematic arm (KA) method allowing fast and extensive measurements of mechanical parameters during treadmill running, has been developed (Belli et al. 1992, 1993). Using this new method, relationships between C_R and C_M have been found in normal as well as in loaded conditions (Belli 1996; Bourdin et al. 1995). However, the KA apparatus has not been used in the fatigued state. The aim of the present study was to examine the physiological and mechanical factors which may be involved in the increase in energy cost during treadmill running to exhaustion.

Methods

Subjects and protocols

A group of 15 healthy triathletes, mean age [26.6 (SD 3.1) years], body mass [71.9 (SD 2.4) kg], height [1.78 (SD 0.04) m], gave written informed consent to participate in this study after all the procedures and possible risks and benefits of participation had been explained to them. The experiment protocol was reviewed and approved by the Human Ethics Committee of Besançon. The best running performances of the subjects over 3000 m, expressed as percentages of the average velocity calculated for the world record, varied from to 80%.

During the three first visits in the laboratory, the subjects ran on a treadmill (Gymrol 2500, Tecmachine, Andrézieux-Bouthéon, France) for a total of three sessions of 10-min duration at 3.5 m · s⁻¹ and five sessions at velocities corresponding to those calculated for their personal record over 3000 m [v_{3000} , mean 4.7 (SD 0.3) m · s⁻¹]. This allowed the subjects to become familiar with treadmill running. During the fourth visit, after a warm up of 10 min at 3.5 m · s⁻¹, the subjects ran to exhaustion at v_{3000} . The subjects were cooled by a fan facing them.

Physiological measurement

Gas exchange was monitored continuously throughout the exhausting exercise. Ventilation (\dot{V}_E), CO₂ production and $\dot{V}O_2$ were recorded breath-by-breath with an automatic gas analyser (CPX

analyser—Medical Graphics Corporation—MSE, Strasbourg, France) and averaged for every minute. A calibration procedure was completed before each test using certified commercial gas preparations. Blood samples were obtained from the antecubital vein (*vena mediana cubiti*) before, immediately after and 3 min after the completion of the exhausting run. As the blood lactate concentrations ($[La^-]_b$) decreased during this 3 min of passive recovery, only $[La^-]_b$ taken immediately at the end of this exercise was retained. The $[La^-]_b$ were measured with a lactate analyser (LA-640 Kontron, Roche Bioelectronics, Basel, Switzerland). During the exhausting run at v_{3000} a non-negligible amount of adenosinetriphosphate could have been synthesised from anaerobic metabolism. Consequently, as proposed by di Prampero et al. (1993) the quantification of the C_R (expressed in joules per kilogram per metre), took into account both aerobic (C_{AER}) and anaerobic compounds (C_{ANA}):

$$C_R = C_{AER} + C_{ANA}$$

The aerobic energy supply was evaluated from the elevation of $\dot{V}O_2$ above basal metabolic rate:

$$C_{AER} = (\dot{V}O_2 - 0.083) \cdot E_{O_2} \cdot v_{3000}^{-1}$$

where $\dot{V}O_2$ is expressed in millilitres per kilogram per second, 0.083 ml · kg⁻¹ is the y -intercept of the $\dot{V}O_2$ -treadmill velocity relationship that has been established by Medbø et al. (1988) in young male adults, E_{O_2} (21.3 J · mlO₂⁻¹) is the energy equivalent of 1 mlO₂ at a respiratory exchange ratio (R) of 1 [during the exhausting run, the mean value of R was 0.99 (SD 0.04)%], and v_{3000} is the mean velocity during contact phase.

The anaerobic energy supply was evaluated from the elevation of $[La^-]_b$ during the exercise ($\Delta[La^-]_b$):

$$C_{ANA} = \Delta[La^-]_b \cdot E_{La} \cdot E_{O_2} \cdot D^{-1}$$

where E_{La} is the O₂ equivalent (3 mlO₂ · mmol⁻¹ · l⁻¹, Margaria et al. 1971; di Prampero et al. 1993) of $\Delta[La^-]_b$ and D is the distance (in metres) covered during the exhausting run. In order that the mechanics and the energy cost of running should not be altered, no blood samples were collected during the exhausting exercise. Based on $[La^-]_b$ that has been measured during an exhausting exercise of 13-min duration (Roston et al. 1987), $\Delta[La^-]_b$ at 4 min was estimated to be 0.25% of $\Delta[La^-]_b$ at the end of exercise.

The work of breathing (W_B , in kilograms per metre per minute) corresponding to \dot{V}_E (in litre per minute) was estimated from the equation that has been proposed by Coast et al. (1993):

$$W_B = 0.251 - 0.0382 \cdot \dot{V}_E + 0.00176 \cdot \dot{V}_E^2$$

Finally, the $\dot{V}O_2$ of the respiratory muscles ($\dot{V}O_{2RM}$, in millilitres per minute) was evaluated as has been suggested by Coast et al. (1993):

$$\dot{V}O_{2RM} = 34.9 + 7.45 \cdot W_B.$$

Mechanical measurements

The mechanical changes were determined using KA. It consisted of four light rigid bars linked by three joints. At each joint, an optical encoder measured the angle between the adjacent segments. It was then possible to compute the instantaneous displacement of the end of KA (the moving end) relative to the fixed end (reference end). The moving end of KA was linked to the subject by a belt fastened around his waist while the reference end was fixed to the ceiling. During running, the measurement errors have been shown to be equivalent to or lower than errors of tracking systems or to film/video analysis (Belli et al. 1993). The displacement of the treadmill belt was measured during the contact phase using an extra optical encoder fixed to a wheel mounted on the treadmill belt with an accuracy of 0.1 mm. The velocity of the treadmill was obtained by a 1st order digital derivation of the displacement signal.

As has been done in previous studies (e.g. Belli et al. 1995), the contact between the foot and the treadmill belt was clearly deter-

mined by a sudden decrease in the treadmill velocity signal. This latter parameter was used to identify the step period. Treadmill and KA encoder signals were collected, at the 4th min and at the end of the exhausting exercise. The signals were recorded on a personal computer (Victor 486 SX33) through a 12-bit data-conversion system especially designed for that purpose. According to the recommendations of Belli et al. (1995), the sampling duration and frequency were 16 s and 100 Hz, respectively (corresponding to 48 ± 4 steps). A 0-phase lag 4th-order Butterworth low pass digital filter with cut-off frequencies of 10 Hz was applied on the KA data. Assuming that the waist movements were a reasonable approximation of centre of mass (CG) displacements as has been proposed by Fenn (1930) and based on trigonometric equations that have been described in detail by Belli et al. (1992), the position of CG was computed.

In the previous studies of Cavagna et al. (1964, 1991) W_{pot} and W_{kin} (expressed in joules per step) have been described as the positive potential energy changes and the positive kinetic energy changes computed for each step, respectively:

$$W_{\text{pot}} = m_b g (h_{\text{max}} - h_{\text{min}})$$

$$W_{\text{kin}} = 0.5 M_b (v_{\text{max}}^2 - v_{\text{min}}^2)$$

where m_b is the body mass (in kilograms), g is the acceleration due to gravity ($9.81 \text{ m} \cdot \text{s}^{-2}$), h_{max} and h_{min} are the maximal and minimal heights of CG (in metres), respectively, v_{max} and v_{min} are the maximal and the minimal horizontal velocities of CG (in metres per second), respectively.

It has been shown that in fast running the potential and kinetic energies do not interchange (Cavagna et al. 1976), and the work due to lateral displacements is negligible (Cavagna et al. 1964), thus the external positive work (W_{ext}) was calculated as:

$$W_{\text{ext}} = W_{\text{pot}} + W_{\text{kin}}$$

Mechanical, kinetic and potential costs (C_M , C_{kin} , C_{pot}) were equal external, kinetic and potential powers divided by the mean velocity of CG during contact, respectively. In addition, the h_{min} of CG was determined.

Statistics

Two sources of intra-individual variability were distinguished:

1. The coefficient of asymmetry between left and right lower limbs (ASY_X , as a percentage) was determined as follows:

$$ASY_X = \sqrt{\frac{(\bar{X}_L - \bar{X})^2 + (\bar{X}_R - \bar{X})^2}{2}} \cdot \bar{X}^{-1} \cdot 100$$

where \bar{X}_L is the mean step value of the left lower limb, \bar{X}_R is the mean step value of the right lower limb, and \bar{X} is the mean of \bar{X}_L and \bar{X}_R .

2. The coefficient of variability (CV_X , percentage) independent of ASY_X was calculated as follows:

$$CV_X = \sqrt{\frac{\sum_{i=1}^{i=n} (X_L - \bar{X}_L)^2 + (X_R - \bar{X}_R)^2}{n-1}} \cdot \bar{X}^{-1} \cdot 100$$

where n is the number of measured steps.

The variables studied were compared in the fatigued and non-fatigued states using a bilateral paired Student's t -test. Linear correlation was used to assess the relationship between C_R and (1) C_M , and (2) the variability in step frequency. Significance was determined from the correlation coefficient. A stepwise regression was performed to identify the possible mechanical determinant of (1) the changes in C_R between non fatigued to fatigued states (2) C_R in the non-fatigued state and (3) C_R in the fatigued state. The C_R was the y variable and the mechanical parameters presented in Table 2 were the x variables. For all tests, significance was declared at $P < 0.05$.

Results

An example of variations in potential and kinetic energies of CG, during four consecutive steps, in the non-fatigued state, is given for subject 1 in Fig. 1. The mean time to exhaustion during the treadmill run, at a mean velocity of 4.53 (SD 0.28) $\text{m} \cdot \text{s}^{-1}$, was 758 (SD 210) s.

Non-fatigued vs fatigued states

Physiological variables

A significant mean increase [6.9 (SD 3.5)%, $P < 0.001$] in C_R from a mean of 4.4 (SD 0.4) $\text{J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$ [0.21 (SD 0.02) $\text{mlO}_2 \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$] to a mean of 4.7 (SD 0.4) $\text{J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$ was observed. The mean proportions of the anaerobic component in C_R were 2.8 (SD 0.7)% and 3.6 (SD 1.5)% in the non-fatigued and fatigued states, respectively. The mean \dot{V}_E increased [19.7 (SD 7.0)%, $P < 0.001$] from a mean of 112.8 (SD 13.9) $\text{l} \cdot \text{min}^{-1}$ to a mean of 135.1 (SD 16.2) $\text{l} \cdot \text{min}^{-1}$ corresponding to a mean increase in $\dot{V}\text{O}_2$ of the respiratory musculature of 66.9 (SD 27.0) $\text{mlO}_2 \cdot \text{min}^{-1}$. The mean O_2 demands of the respiratory muscles represented 4.3 (SD 0.5)% and 5.6 (SD 0.8)% of C_R in the non-fatigued and fatigued states, respectively. The mean $[\text{La}]_b$ increased ($P < 0.001$) from a pre-exercise value of 2.6 (SD 0.7) $\text{mmol} \cdot \text{l}^{-1}$ to 11.0 (SD 2.3) $\text{mmol} \cdot \text{l}^{-1}$ in the fatigued state (Table 1).

Mechanical variables

Detailed analysis of mechanical parameters, in the fatigued and non-fatigued state is presented in Table 2. A significant mean increase in C_M [17.0 (SD 26.0)%, $P < 0.05$] from a mean of 2.36 (SD 0.23) $\text{J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$ to a mean of 2.74 (SD 0.55) $\text{J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$ was noted. The mean \dot{W}_{kin} increased significantly [21.0 (SD 34.4)%,

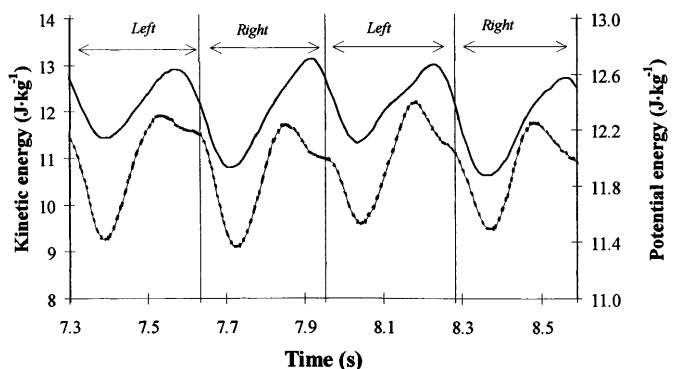


Fig. 1 Example of the changes in kinetic (dashed line) and potential (solid line) energies for subject 1, in the non-fatigued state. For clarity, only four steps are shown. The vertical lines indicate the beginning of the contact between the foot and the treadmill belt

Table 1 Physiological variables in the non-fatigued and fatigued states and mean changes. $\dot{V}O_2$ O_2 Uptake, $[La^-]_b$ blood lactate concentration, C_R energy cost of running (aerobic + anaerobic component), \dot{V}_E minute ventilation

Variable	Non-fatigued state		Fatigued state		Mean change		
	Mean	SD	Mean	SD	Mean	SD	
$\dot{V}O_2$ ($ml \cdot kg^{-1} \cdot min^{-1}$)	59.7	4.03	62.7	3.8	5.0%	1.8%	***
$[La^-]_b$ ($mmol \cdot l^{-1}$)	2.6	0.7	11.0	2.3	347.3%	145.9%	***
C_R ($J \cdot kg^{-1} \cdot m^{-1}$)	4.4	0.4	4.7	0.4	6.9%	3.5%	***
\dot{V}_E ($ml \cdot kg^{-1} \cdot min^{-1}$)	112.8	13.9	135.1	16.2	19.7%	7.0%	***

*** $P < 0.001$ for paired Student's t -test

Table 2 Mechanical variables in the non-fatigued and fatigued states and mean changes. h_{min} minimal height of the centre of mass, SF step frequency, CV_{SF} variability of SF independent of asymmetry between left and right lower limbs, ASY_{SF} asymmetry SF between left and right lower limbs, C_{kin} kinetic cost of running,

$CV_{C_{kin}}$ variability of C_{kin} , C_{pot} potential cost of running, $CV_{C_{pot}}$ variability of C_{pot} , C_M mechanical cost of running, CV_{C_M} variability of C_M independent of asymmetry between left and right lower limbs, ASY_{C_M} asymmetry between left and lower limbs

Variables	Non-fatigued state		Fatigued state		Mean change		
	Mean	SD	Mean	SD	Mean	SD	
h_{min} (m)	1.06	0.05	1.04	0.08	-1.8%	6.9	
SF (Hz)	3.05	0.11	3.00	0.13	-1.8%	2.6	*
CV_{SF} (%)	2.80	0.50	3.29	0.78	19.3%	27.8	*
ASY_{SF} (%)	1.97	1.55	2.09	1.65	149.3%	358.6	
C_{kin} ($J \cdot kg^{-1} \cdot m^{-1}$)	1.89	0.23	2.26	0.57	21.0%	34.4	*
$CV_{C_{kin}}$ (%)	8.74	2.14	10.76	2.56	28.2%	41.4	*
C_{pot} ($J \cdot kg^{-1} \cdot m^{-1}$)	0.47	0.06	0.48	0.07	2.3%	12.9	
$CV_{C_{pot}}$ (%)	7.49	1.19	9.89	4.10	31.4%	46.8	*
C_M ($J \cdot kg^{-1} \cdot m^{-1}$)	2.36	0.23	2.74	0.55	17.0%	26.0	*
CV_{C_M} (%)	6.69	1.67	8.77	3.06	38.4%	62.8	*
ASY_{C_M} (%)	4.43	4.75	8.13	9.61	338.7%	791.8	

* $P < 0.05$, ** $P < 0.01$ for paired Student's t -test

$P < 0.05$] from a mean of 1.89 (SD 0.23) $J \cdot kg^{-1} \cdot m^{-1}$ to 2.26 (SD 0.57) $J \cdot kg^{-1} \cdot m^{-1}$; while mean C_{pot} remained unchanged [0.47 (SD 0.06) $J \cdot kg^{-1} \cdot m^{-1}$ vs 0.48 (SD 0.07) $J \cdot kg^{-1} \cdot m^{-1}$]. For C_M , mean variability and asymmetry increased from 6.7 (SD 1.7)% to 8.8 (SD 3.1)% ($P < 0.05$), and from 4.4 (SD 4.8)% to 8.1 (SD 9.6)% ($P > 0.05$), respectively. A significant mean decrease [1.8 (SD 2.6)%], $P < 0.05$] in step frequency from a mean of 3.05 (SD 0.11) Hz to a mean of 3.00 (SD 0.13) Hz was observed. For this parameter, mean variability increased [19.3 (SD 27.8)%], $P < 0.05$] from a mean of 2.80 (SD 0.50)% to a mean of 3.29 (SD 0.78)%.

Relationship between C_R and mechanical parameters

A significant correlation between C_R and C_M was found ($r = 0.68$, $P < 0.01$; Fig. 2) in the non-fatigued state; while, only a non-significant ($r = 0.25$, NS; Fig. 2) tendency was noted in the fatigued state. Significant correlations between C_R and the variability in step frequency were found, in the non-fatigued ($r = 0.69$, $P < 0.01$) and fatigued states ($r = 0.58$, $P < 0.05$, Fig. 2).

In the non-fatigued state, the mechanical variables retained in the stepwise regression were (1) the vari-

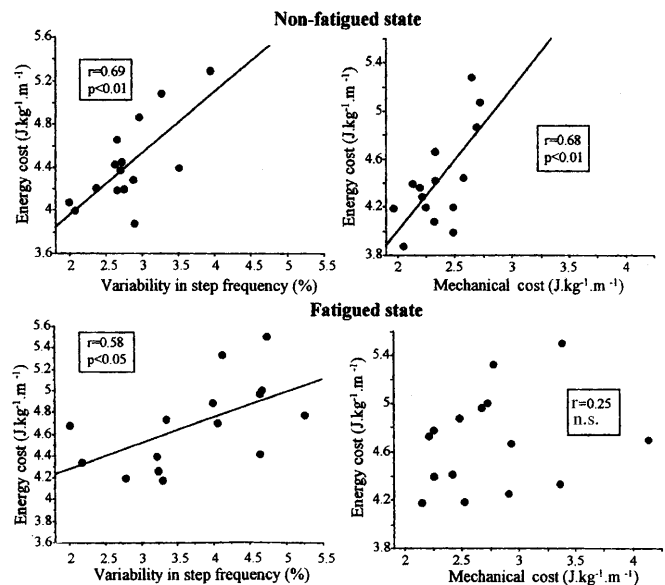
**Fig. 2** Correlations between the energy cost of running and (i) the variability in step frequency (variability independent of that due to asymmetry) and (ii) the mechanical cost of running in non-fatigued and fatigued states

Table 3 Summary of the stepwise regression between energy cost of running (y variable) and mechanical variables (x variables given in **Table 2**) in the non-fatigued (**A**) and in fatigued state (**B**) CV_{SF} Variability in step frequency (variability independent of asymmetry), C_M mechanical cost of running, h_{min} minimal height of the centre of mass

Step no.	Variable entered removed	r	r^2	Increase in r^2	P
A. Non-fatigued state					
1	CV_{SF} (%)	0.69	0.49	0.45	
2	C_M ($J \cdot kg^{-1} \cdot m^{-1}$)	0.85	0.72	0.71	< 0.01
B. Fatigued state					
1	CV_{SF} (%)	0.58	0.32	0.28	
2	h_{min} (m)	0.73	0.52	0.44	< 0.01

ability in the step frequency and (2) C_M (Table 3). In the fatigued state, the mechanical variables retained were (1) variability in step frequency and (2) the h_{min} of CG (Table 3).

Changes in C_R and changes in mechanical parameters

No correlation was found between the changes in C_R and the changes in C_M . The mechanical variables retained in the stepwise regression were (1) the variability in the step frequency and (2) the variability in the potential cost (Table 4).

Discussion

The values of C_R and C_M in the non-fatigued state were greater than those that have been reported in previous studies using similar methods (Bourdin et al. 1995; di Prampero et al. 1993; Lacour et al. 1990). This difference is probably due to the facts that in the present study:

1. The running velocity was evaluated from the mean velocity of CG during contact, and
2. The value of the energy equivalent of 1 mlO₂ was higher than in previous studies.

Because treadmill velocity artificially increases during the flight phase compared to real locomotion, the mean velocity during the whole of the step has been shown to be greater than that determined during contact (Lacour 1996). As R reached 1 in the present study, the value of

Table 4 Summary of stepwise regression between changes in energy cost of running (y variable) and changes in mechanical variables (x variables given in **Table 2**). The changes were normalised with respect to the non-fatigued state values. CV_{SF} Variability in step frequency (variability independent of asymmetry), $CV_{C_{pot}}$ variability in the potential cost

Step no.	Variable entered removed	r	r^2	Increase in r^2	P
Non-fatigued state					
1	CV_{SF} (%)	0.64	0.42	0.37	
2	$CV_{C_{pot}}$ (%)	0.77	0.59	0.53	< 0.01

the energy equivalent utilised ($21.3 J \cdot mlO_2^{-1}$) was higher than in previous studies (e.g. $20.9 J \cdot mlO_2^{-1}$, corresponding to $R = 0.96$; Bourdin et al. 1995; di Prampero et al. 1993).

In the non-fatigued state, the relationship obtained between C_R and C_M agreed with that reported by Bourdin et al. (1995). It confirmed that the lack of relationship mentioned in other studies (e.g. Morgan et al. 1990) was probably due to the limited number of steps analysed with respect to the variability of the mechanical parameters in running (Belli et al. 1995). The amplitude of the increase in C_R found in the present study was similar to that reported after an experimental marathon (Brueckner et al. 1991), and during a triathlon run completed at racing pace compared to a 10 000 m run (Guezennec et al. 1996).

Respiratory muscle $\dot{V}O_2$

It has been suggested that the increase in energy expenditure of the respiratory muscles could explain the C_R increase (Poole et al. 1991). The work of breathing increases any time that ventilation is increased. The energy demand is enlarged as well. Based on the equations that have been proposed by Coast et al. (1993), the increase in respiratory muscle $\dot{V}O_2$ evaluated from the increase in \dot{V}_E found in the present study explained a considerable proportion [mean 25.2 (SD 10.4)%] of the increase in C_R . It has been reported (Guezennec et al. 1996) that a triathlon run elicited a significantly higher \dot{V}_E and C_R 16.2% and 7.1%, respectively, compared to a 10 000 m run. The increase in respiratory muscle $\dot{V}O_2$ recalculated from these data, would explain about 10% of the C_R increase. This smaller proportion compared with that found in the present study could be due to the lower mean exercise intensity sustained over 10,000 m (Guezennec et al. 1996) than over 10,000 m (present study).

One of the physiological mechanisms of the increase in C_R due to the rise in \dot{V}_E could reside in the change in oxygen diffusion across the alveolar-capillary membrane that has been observed during heavy exercise in trained athletes (Caillaud et al. 1995). It has been shown that the change of pulmonary diffusion is mainly due to an

increase in blood pressure resulting in lesions of vessel walls and in the leakage of plasma into the space separating the vessels from the alveolar membrane (Caillaud et al. 1995).

Mechanical cost of running

A second possible explanation of the C_R increase is an increase in the mechanical work per unit of distance. In the fatigued state, both C_R and C_M increased. However, the fact that firstly no correlation could be found between the changes in C_R and the changes in C_M and that secondly in the fatigued state, only a tendency was noted in the relationship between C_R and C_M would indicate that running economy is not solely dependent on the external work done per unit of distance. When respiratory muscle $\dot{V}O_2$ was subtracted from C_R , the relationship between C_R and C_M , in the fatigued state, was slightly enhanced but remained non-significant.

Other parameters linked to muscle fatigue may obscure the relationship between running economy and C_M in these particular conditions. One could argue that a change in the internal mechanical work could also explain the increase in C_R . For a given running velocity, internal work has been found to increase as a function of step frequency (Cavagna et al. 1991). In the present study, the small variation (-1.8%) in step frequency found between the non-fatigued and fatigued states would indicate that the change in the internal work was negligible. Furthermore, since step frequency decreased slightly in the fatigued state, the internal work would tend to decrease slightly which is not compatible with an increase in C_R .

Step variability and regulation of lower limb stiffness

Step variability in running is an interesting phenomenon that demonstrates consistent relationships with C_R . The results of the present study confirm the relationship between C_R and step variability observed by Belli et al. (1995).

It may be proposed that an inaccurate control of step frequency could explain the increase in C_R . As has been mentioned in animal locomotion (Taylor 1985), and in human running (Cavagna et al. 1991; Dalleau et al. in press) step frequency has to be controlled very accurately to match the optimal step frequency. This step frequency has been shown to optimise leg stiffness and thus energy expenditure at a given velocity (Cavagna et al. 1991; Kaneko 1987; Taylor 1985). According to Komi et al. (1992), an inability to control accurately leg stiffness could decrease the efficiency of the storage and recoil of energy.

Because high variability is not favourable for maintaining an optimal step frequency, the increase in step frequency variability observed in the fatigued condition and the relationship between the changes in step vari-

ability and the changes in C_R could partly explain the increase in C_R . However, such deficiency between optimal and freely chosen step frequency should result in a decreased muscle efficiency (see Kaneko 1987). In the present study, the C_M displayed a more marked increase than C_R , indicating an increase of the external efficiency ($C_M \cdot C_R^{-1}$). Although this increase was not significant, it seems that other mechanisms responsible for the increase of both C_R and external efficiency could be involved. It is worth noting that during contact the height of CG tended to decrease mean [2 (SD 7) cm] with fatigue. Furthermore, in the fatigued condition, the stepwise regression showed a relationship between C_R and h_{\min} . It could then be hypothesised that when fatigued, the subjects of the present study were running *seated* trying to compensate for their lower active stiffness by stretching their leg extensors. However, further studies have to be conducted to elucidate the underlying mechanisms of the relationship between C_R and mechanical changes occurring with fatigue.

Conclusion

Both physiological and biomechanical variables appear to affect the energy cost in the fatigued state. The increase in $\dot{V}O_2$ of respiratory muscles explained about 25% of the increase in C_R in the fatigued state. The external mechanical work could partly explain the increase in C_R . The results further suggest that the increase in C_R could also have been due to an increase of step variability and to a modified stretch of the leg extensor muscles.

Acknowledgements The authors wish to express their thanks to Dr V. Buchet, M. Groetz, Dr F. Guillaume, Dr J. Callier for their technical assistance and to the subjects for their cooperation.

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