

Influence of the world's most challenging mountain ultra-marathon on energy cost and running mechanics

Gianluca Vernillo · Aldo Savoldelli · Andrea Zignoli ·
Pietro Trabucchi · Barbara Pellegrini ·
Grégoire P. Millet · Federico Schena

Received: 18 September 2013 / Accepted: 15 January 2014 / Published online: 30 January 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract

Purpose To examine the effects of the world's most challenging mountain ultra-marathon (Tor des Géants® 2012) on the energy cost of three types of locomotion (cycling, level and uphill running) and running kinematics.

Methods Before (pre-) and immediately after (post-) the competition, a group of ten male experienced ultra-marathon runners performed in random order three submaximal 4-min exercise trials: cycling at a power of 1.5 W kg⁻¹ body mass; level running at 9 km h⁻¹ and uphill running at 6 km h⁻¹ at an inclination of +15 % on a motorized treadmill. Two video cameras recorded running mechanics at different sampling rates.

Results Between pre- and post-, the uphill-running energy cost decreased by 13.8 % ($P = 0.004$); no change was noted in the energy cost of level running or cycling (NS). There was an increase in contact time (+10.3 %, $P = 0.019$) and duty factor (+8.1 %, $P = 0.001$) and a decrease in swing time (−6.4 %, $P = 0.008$) in the uphill-running condition.

Conclusion After this extreme mountain ultra-marathon, the subjects modified only their uphill-running patterns for a more economical step mechanics.

Keywords Cycling · Fatigue · Kinematics · Oxygen cost · Running · Ultra trail

Abbreviations

θ_A (°)	Ankle angle
$\dot{V}CO_2$ (L min ⁻¹)	Carbon dioxide output
t_c (s)	Contact time
CT (s)	Cycle time
DF (%)	Duty factor
EC	End of contact
C_{cycl} (kJ L ⁻¹)	Energy cost of cycling
C_r (J m ⁻¹ kg ⁻¹)	Energy cost of running
MUM	Extreme mountain ultra-marathon
θ_F (°)	Foot angle
GE (%)	Gross efficiency
IC	Initial contact
θ_K (°)	Knee angle
\dot{W}_{vert} (W kg ⁻¹)	Mechanical work rate
$\dot{V}O_2$ (L min ⁻¹)	Oxygen uptake
$\dot{V}E$ (L min ⁻¹)	Pulmonary ventilation
t_c^{-1} (s ⁻¹)	Rate of force application
RER	Respiratory exchange ratio
θ_L (°)	Shank angle
SF (Hz)	Stride frequency
SL (m)	Stride length
t_s (s)	Swing time
θ_T (°)	Thigh angle
$\dot{V}E/\dot{V}CO_2$	Ventilatory equivalent ratio for carbon dioxide
$\dot{V}E/\dot{V}O_2$	Ventilatory equivalent ratio for oxygen

Communicated by Jean-René Lacour.

G. Vernillo · A. Zignoli · B. Pellegrini · F. Schena
Department of Neurological and Movement Sciences, University
of Verona, Verona, Italy

G. Vernillo (✉) · A. Savoldelli · A. Zignoli · P. Trabucchi ·
B. Pellegrini · F. Schena
CeRiSM, Research Center 'Sport, Mountain and Health',
University of Verona, via Matteo del Ben, 5/b, 38068 Rovereto,
TN, Italy
e-mail: gianluca.vernillo@univr.it

G. P. Millet
Department of Physiology, Faculty of Biology and Medicine,
ISSUL, Institute of Sport Sciences, University of Lausanne,
Lausanne, Switzerland

Introduction

A growing body of literature on the physiological and biomechanical changes associated with ultra-endurance running events [any event involving distances longer than the classic marathon of 42.195 km (Knechtle 2012)] (Millet et al. 2000, 2002, 2011a; Morin et al. 2011; Lazzer et al. 2012; Gimenez et al. 2013; Saugy et al. 2013) indicates that runners experience long-term fatigue after such events. This complex phenomenon alters running step mechanics and spring-mass behavior (Millet et al. 2000, 2009b; Morin et al. 2011; Degache et al. 2013), leading to ‘safer’ running patterns (Morin et al. 2011) that reduce the deleterious effects of ultra-distance running and minimize muscle-joint damage (Millet et al. 2009b). However, whether such alterations are also responsible for changes in the energy cost of running (C_r) remains debated and it is not yet clear whether limiting the muscle damage and/or muscular fatigue associated with ultra-endurance running positively (or negatively) affect C_r (Millet et al. 2000, 2012; Millet 2012).

C_r [the amount of energy spent to transport the subject’s body over one unit of distance (di Prampero et al. 2009)] has been reported to increase with the distance covered (Brückner et al. 1991) during simulated competitions shorter than or equal to the classic marathon distance (Nicol et al. 1991a, b; Kyröläinen et al. 2000; Hunter and Smith 2007). The results for longer distances are ambiguous, however. C_r was not found to increase after a 65-km ultra-marathon (Millet et al. 2000), but it did increase by about 18 % for exercises lasting more than 7 h (Lazzer et al. 2012) and by about 6 % during a 24-h treadmill run (Gimenez et al. 2013) and after running 8,500 km in 161 days (Millet et al. 2009b).

But because these studies measured C_r under a level-running protocol, their results may not be inferred to extreme mountain ultra-marathon (MUM) runs, which are usually characterized by an extreme distance over rough terrain and a large positive/negative elevation change along their course. Such events offer a unique opportunity to investigate the human body’s limits in physiological and adaptive responses (Millet and Millet 2012). For example, the alterations in neuromuscular function found after MUMs (Millet et al. 2011b; Saugy et al. 2013) suggest changes in muscle recruitment patterns and in the energy cost associated with extreme fatigue.

As compared to level running, running uphill may require an increased amount of muscle work to increase the potential energy of the body with each stride (Higham and Biewener 2008), as observed by the increased ratio between positive (concentric) and negative (eccentric) external work (Minetti et al. 1994). Hence, the greater contribution of concentric muscle activation during uphill running elicits greater metabolic strain (Pringle et al. 2002; Snyder and Farley 2011; Snyder et al. 2012). Accordingly,

C_r may increase noticeably when running uphill as compared to level running because of the additional mechanical work done against gravity (Taylor et al. 1972). Also, differences in running mechanics have been noted between uphill and level locomotion (Padulo et al. 2013).

Moreover, the energy cost alterations associated with the extreme fatigue after a MUM event may differ between running and cycling. Several physiological differences between running and cycling exist: heart rate differs between the two activities at both maximal and submaximal intensities; delta efficiency (the ratio of an increment in external mechanical power output to the increase in metabolic power required to produce it) is higher in running; ventilation is more impaired in cycling than in running due to mechanical constraints; and central fatigue and decreased maximal strength are more pronounced after prolonged exercise in running than in cycling (Millet et al. 2009a). Furthermore, the mode of muscle activation is predominantly concentric in cycling and uphill running, whereas eccentric muscle action still plays an important role during level running (Bijker et al. 2002). However, because it is unclear whether the energy cost is influenced by mechanical or metabolic adaptations, the question whether the energy cost may present the same behavior during cycling and uphill running after a MUM remains open.

Over the years, researchers have focused their attention on the hematological (Schobersberger et al. 1996), neuromuscular (Millet et al. 2011b; Saugy et al. 2013), biomechanical (Morin et al. 2011) and myocardial (Vitiello et al. 2013) changes following a MUM. But none to date have assessed the effects of an event, in which athletes must complete the race in 70–150 h, on the energy cost of different types of locomotion and running kinematics.

In the present study, we analyzed the changes in the energy cost of three types of locomotion (cycling, level and uphill running) and running patterns in a group of runners that participated in the world’s most challenging mountain ultra-marathon (Tor des Géants® 2012), which is mainly characterized by gradient locomotion. Furthermore, we tested the hypothesis that after such an ultra-distance event athletes experience an extreme fatigue state constraining them to adjust their movement patterns, leading to concomitant alterations in C_r , as observed in previous studies of shorter running tasks (Cavanagh and Williams 1982; Nelson 1983; Cavanagh and Kram 1985; Hunter and Smith 2007).

Methods

Subjects

The race organizer invited the male runners to take part in the present study through an announcement posted on the event website. Twenty-seven experienced ultra-marathon runners

voluntarily participated. They were tested twice, before and then after the run. Of the 27 initially interested participants, 18 (66.7 %) completed the MUM. The finishers: starters ratio for our subjects was similar to the ratio reported by Saugy et al. (2013) for this race. Due to the extreme fatigue the subjects experienced during the post-testing sessions, not all of them completed all three test protocols. Two subgroups were formed: one included the subjects who completed all three tests ($n = 7$) and the second included those who completed two tests ($n = 10$). One subject completed only one test and was, therefore, excluded from the final analysis (see the experimental overview for more details) (Table 1).

Prior to the pre-test session, a questionnaire was administered to collect data on the subjects' training experience. On average, the subjects had 10.5 ± 3.5 years of training in running and 4.5 ± 1.5 years of ultra-endurance experience. The training sessions in preparation for the race consisted of 3–4 sessions per week with 7.5 ± 3.0 h per week of training. All subjects were fully informed of the procedure and the risks involved and signed a written informed consent outlining study requirements before data collection. The experiment was conducted according to the Declaration of Helsinki and approval was obtained from the institutional Ethics Committee of the University of Verona, Italy (Department of Neurological and Movement Sciences).

Race characteristics

The course of the Tor des Géants® is 330 km long, over rough terrain and with considerable positive/negative

elevation change (+24,000 m), around the territory of Valle d'Aosta (Italy). There were 563 starters and 354 finishers (63 %) in the 2012 race. The altitude along the course ranges between 3,300 and 322 m, with 20 mountain passes over 2,000 m (Fig. 1). The maximum time allowed for completion of the race is 150 h, and the current record is 75 h 56 min 31 s. The distance is divided into seven stages with six aid-stations where runners can rest and sleep. The organizing committee imposes no rules regarding rest stops, and the winner is the runner who completes the race in the shortest time, deciding on when and how long to stop for rest and feeding (<http://www.tordesgeants.it/en/content/regulation>).

Experimental overview

A longitudinal, within-group paired comparison design was used. Subjects underwent two test sessions: the first was performed 1–2 days preceding the race (pre-), and the second immediately after the race (post-). Shortly after the subjects crossed the finishing line, they were brought by car to the laboratory (~1 km away). Prior to pre- and post-testing procedures, body mass was measured to the nearest 0.1 kg using a digital scale so as to determine the cycling workload. All subjects were familiar with motorized treadmill running and cycling on a cycle ergometer. Pre- and post-sessions were organized in a similar fashion. All subjects wore specific trail-running shoes (Category A5). After apparatus calibration, gas exchange was measured at rest for 4 min in an upright position. Testing was performed in

Table 1 Mean (\pm SD) and range of the characteristics of the subjects who completed the competition ($n = 10$)

		Age (years)	Stature (cm)	Body mass (kg)		BMI (kg m^{-2})	
				Pre-	Post-	Pre-	Post-
	$n = 7$						
There was no significant difference between the two groups ($n = 7$ and $n = 10$) for any of the characteristics ($P > 0.05$)	Mean	40.6	177.4	71.5	71.4	22.8	22.7
	SD	10.8	4.1	7.1	7.1	2.6	2.3
	Range	24–55	173–183	60.1–82.7	59.6–81.4	19–27	18.8–26.6
	$n = 10$						
There were no statistical differences in body mass and BMI (BMI) between the pre- and post-race ($P > 0.05$)	Mean	41.5	177.5	71.3	71.3	22.6	22.6
	SD	10.6	3.6	6.0	6.3	2.4	2.3
	Range	24–53	173–183	60.1–82.7	59.6–81.4	19–27	18.8–26.6

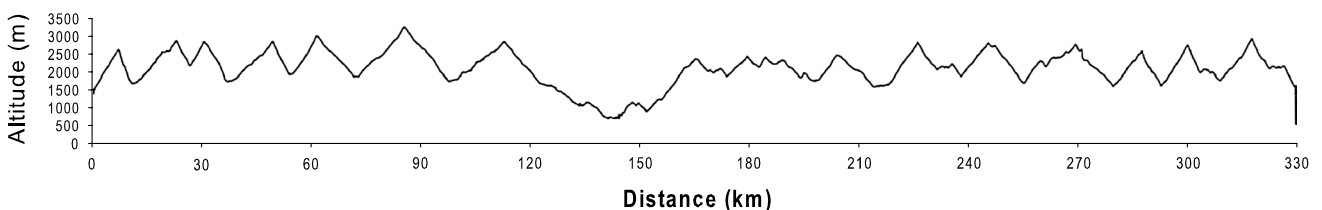


Fig. 1 The course of the MUM

random order in three different conditions: (1) a 4-min bout on a cycle ergometer (Lode Excalibur Sport, Lode, Groningen, NL) at a power of 1.5 W kg^{-1} body mass with a pedal cadence at 80 rpm (Millet et al. 2000) to determine whether differences in the energy cost are related to mechanical or metabolic factors; (2) a running bout of 4 min at 9 km h^{-1} (2.5 m s^{-1}) at 0 % to determine differences in the energy cost between uphill and level running; and (3) another running bout of 4 min at 6 km h^{-1} (1.7 m s^{-1}) on a motorized treadmill (RunRace, Technogym, Gambettola, Italy) at an inclination of +15 % (9°). Seven subjects completed the three tests and ten subjects (7 + 3 subjects) completed the cycling and the uphill-running tests. Based on the observations by Millet et al. (2000), the intensities of the three conditions were selected to maximize comfort. Data on kinematic variables were acquired using two video cameras placed perpendicular to the subject's sagittal plane which recorded the subject's movement at two sampling rates.

Energy cost

The physiological parameters were filtered into 3-s blocks for analysis. Due to the time it takes for an individual to reach a physiological steady-state condition and for the indirect calorimetry measurement (Quark b2, Cosmed, Rome, Italy) to reflect actual energy cost, the first 3 min of each 4-min measurement was discarded in the analysis and the last 1-min sets were averaged. The data included: oxygen uptake ($\dot{V}O_2$), carbon dioxide output ($\dot{V}CO_2$), pulmonary ventilation ($\dot{V}E$), ventilatory equivalent ratio for oxygen ($\dot{V}E/\dot{V}O_2$), ventilatory equivalent ratio for carbon dioxide ($\dot{V}E/\dot{V}CO_2$), and respiratory exchange ratio (RER, where $RER = \dot{V}CO_2/\dot{V}O_2$). The energy cost of cycling (C_{cycl}) was calculated as the power output divided by the rate of $\dot{V}O_2$ and expressed as kJ L^{-1} ; gross efficiency (GE) was calculated according to Moseley and Jeukendrup (2001). The net C_r was calculated from the ratio between the difference in $\dot{V}O_2$ at steady state minus $\dot{V}O_2$ at rest and the speed maintained during the test. This value was expressed in $\text{J m}^{-1} \text{kg}^{-1}$ by converting the net $\dot{V}O_2$ to the corresponding metabolic energy output using an energy equivalent of O_2 ranging from 21.13 to 19.62 kJ L^{-1} depending on the RER. For the uphill-running condition, the mechanical work rate (\dot{W}_{vert} , W kg^{-1}) was assessed according to Minetti et al. (2002).

Kinematics data acquisition

Data on the subject's movement were acquired using two video cameras placed perpendicular to the subject's sagittal plane on his right side. Specifically, a high frequency camera (Canon PowerShot SX 230 HS, Canon Inc., Tokyo, Japan) (sampling rate, 120 Hz) recorded the lower

part of the subject's body to capture the stride characteristics; a second camera (Sony HandyCam HDR-HC1E HDV 1080i, Sony Corp., Tokyo, Japan) (sampling rate, 50 Hz) filmed the whole subject's leg to acquire data on the grades of the lower limb segments. The cameras were calibrated by filming a rigid box before the beginning of each test session. The box was equipped with four markers (at each of the four corners) and placed on the treadmill. The box dimensions were comparable with those spanned by the subjects during the experiment (63 cm height and 35 cm base). The motion of each lower limb segment was tracked by means of four round, reflective markers (diameter, 1.9 cm) attached to the greater trochanter, lateral femoral condyles, lateral malleoli, and fifth metatarsal head. With this setup, three rigid body segments were defined: thigh, shank, and foot (see Fig. 2 for details). For the fifth metatarsal, the marker was placed on the running shoe at the position best projecting the anatomical landmark. The markers were secured to the skin and the running shoe with adhesive spray and double-sided adhesive discs. All markers remained in the same position throughout the testing session. The procedures were conducted by the same

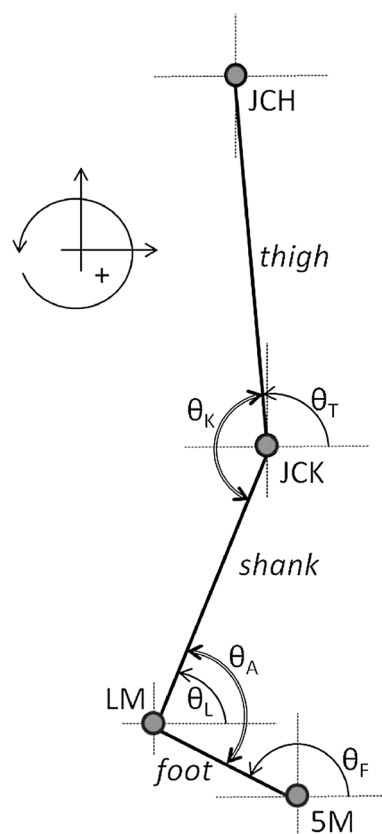


Fig. 2 Schematic representation of the definition of the angular measurements. *JCH* joint center of the hip, *JCK* joint center of the knee, *LM* lateral malleolus, *5M* fifth metatarsal. θ_T thigh angle, θ_L shank angle, θ_F foot angle, θ_K knee angle, θ_A ankle angle

experienced investigator according to standardized procedures (Cappozzo et al. 1995). Running data acquisition lasted 30 s and was performed at least 2 min after the start of each test session to allow stabilization of the individual subject's gait.

Coordinate data represent the spatial location of the lateral aspect of the head of the fifth metatarsal and the lateral malleolus and the joint center of the knee and the hip. Coordinate data were calculated using SIMI motion software (version 7.5.307, Simi Reality Motion System GmbH, Unterschleißheim, Germany) frame by frame for both cameras. The data were then exported into a text file format for processing in a numerical computing environment (Matlab version R2012a, The MathWorks Inc., Natick, MA, USA). All variables refer to the right side of the body.

Kinematics data processing

Kinematic measures calculated from the coordinate data included: contact time (t_c), duty factor (DF), rate of force application (t_c^{-1}), swing time (t_s), cycle time (CT), stride frequency (SF = 1 CT⁻¹), and stride length (SL = CT speed) (Winter 2009).

From the recording of the second camera, the coordinate values allowed to determine the absolute angles formed by the body segments with respect to the horizontal and relative joint angles [thigh angle (θ_T), shank angle (θ_L), foot angle (θ_F), knee angle (θ_K), and ankle angle (θ_A)] (see Fig. 2 for details) (Winter 2009). Frame-by-frame data analysis identified the beginning and the end of the contact period, and each parameter was considered at the initial contact (IC) and end of contact (EC).

The data from the camera recordings were obtained from at least five consecutive gait cycles during the last 1 min of each running condition and then averaged.

Statistical analysis

Data are expressed as mean \pm standard deviation (SD). Results were tested for normal distribution using the Shapiro–Wilk W test. To determine possible differences between the different energy costs, each value was transformed to a z score [$z = (\text{raw score} - \text{mean}) \cdot \text{SD}^{-1}$] using the variable specific grand mean and SD. The means for standardized values were then compared using one-way ANOVA with post hoc Bonferroni's procedures. Each variable was analyzed using a paired sample t test (t) to determine possible differences between pre- and post-MUM. Pearson's product moment correlation coefficient (r) with 90 % confidence intervals (CI) was used to examine the relationships between selected parameters. The magnitude of the changes was assessed using effect size (ES) statistic with 90 % CI and percentage change. The ES was classified as

follows: <0.2 = trivial, 0.2 – 0.6 = small, 0.6 – 1.2 = moderate, 1.2 – 2.0 large, >2.0 = very large. Statistical analyses were performed using IBM™ SPSS™ Statistics (version 20.0.0, IBM Corporation, Somers, NY, USA), and the significance level was set at $P < 0.05$.

Results

The time of the winner of this MUM race was 75 h 56 min 31 s and the average time of the study subjects was 118 h 28 min 26 s (range 102 h 46 min 28 s–135 h 41 min 40 s; ranking, 79th–329th). There was no significant difference between the two groups of 10 and 7 subjects in age, height, body mass or body mass index (BMI). There were no statistical differences in body mass or BMI between the pre- and post-race sessions or between the different post-energy costs. The $\dot{V}O_2$ response to exercise was similar for all three testing conditions. A steady-state $\dot{V}O_2$ was attained within 3 min for each condition.

Energy cost

Table 2 reports the cycling test results: post- $\dot{V}E$ increased by 17.4 % ($t = -3.3$, $P = 0.01$, ES = 0.94 ± 0.53), $\dot{V}E/\dot{V}O_2$ by 14.5 % ($t = -3.2$, $P = 0.01$, ES = 1.01 ± 0.57), and $\dot{V}E/\dot{V}CO_2$ by 22.4 % ($t = -5.0$, $P = 0.001$, ES = 1.58 ± 0.57). There were no significant changes in C_{cycl} or GE between the pre- and post-test sessions.

The level-running test results are presented in Table 3. There were no significant changes in C_r between the pre- and post-test sessions. Only $\dot{V}E$, $\dot{V}E/\dot{V}O_2$ and $\dot{V}E/\dot{V}CO_2$ significantly increased by 11.8 % ($t = -2.7$, $P = 0.04$, ES = 0.98 ± 0.71), 17.2 % ($t = -3.1$, $P = 0.02$, ES = 0.97 ± 0.60), and 21.7 % ($t = -5.7$, $P = 0.001$, ES = 1.32 ± 0.44), respectively.

Table 4 reports the uphill-running test results. Post- C_r decreased by 13.8 % ($t = 3.8$, $P = 0.004$, ES = -1.0 ± 0.48). Conversely, post- $\dot{V}E$ was 17.9 % higher ($t = -3.8$, $P = 0.004$, ES = 0.94 ± 0.45), post- $\dot{V}E/\dot{V}O_2$ rose by 21.6 % ($t = -2.8$, $P = 0.02$, ES = 0.94 ± 0.62), and post- $\dot{V}E/\dot{V}CO_2$ increased by 29.2 % ($t = -6.2$, $P < 0.001$, ES = 1.75 ± 0.52).

Kinematics data

No difference was detected in the kinematics data during the level-running condition (Table 5). Table 6 reports the uphill-running results: t_c increased by 10.3 % ($t = -2.8$, $P = 0.019$, ES = 0.61 ± 0.39) and DF by 8.1 % ($t = -5.1$, $P = 0.001$, ES = 1.03 ± 0.37); t_s decreased from pre- to post-test session by 6.4 % ($t = 3.4$, $P = 0.008$, ES = -0.68 ± 0.36). In the kinematics data, θ_F increased

Table 2 Changes in the metabolic variables measured during the cycling condition at a power of 1.5 W kg⁻¹ body mass before (pre-) and after (post-) the MUM (*n* = 10)

Variable	Pre-			Post-			% Change	ES	±90 % CI
	Mean	SD	Range	Mean	SD	Range			
C_{cycl} (kJ L ⁻¹)	5.101	0.42	4.30–5.90	5.105	0.45	4.27–5.80	0.08	+0.01 (trivial)	0.13
GE (%)	15.97	1.18	13.90–17.50	15.63	0.84	14.70–16.90	-1.77	-0.30 (small)	0.29
$\dot{V}E$ (L min ⁻¹)	53.9	8.5	43.3–66.5	62.5*	8.3	49.6–73.7	+17.4	+0.94 (large)	0.53
$\dot{V}O_2$ (L min ⁻¹)	1.9	0.2	1.6–21.2	1.8	0.5	0.4–2.2	-5.0	-0.19 (trivial)	0.62
$\dot{V}CO_2$ (L min ⁻¹)	1.8	0.2	1.5–2.1	1.6	0.5	0.3–2.0	-10.9	-0.44 (small)	0.57
$\dot{V}E/\dot{V}O_2$	27.8	2.5	22.7–31.0	31.8*	4.4	25.8–40.0	+14.5	+1.01 (large)	0.57
$\dot{V}E/\dot{V}CO_2$	29.4	2.5	25.5–32.5	36.0*	4.7	28.6–45.0	+22.4	+1.58 (large)	0.57
RER	0.94	0.06	0.89–1.00	0.91	0.07	0.89–1.00	-5.5	-0.73 (moderate)	0.45

C_{cycl} energy cost of cycling, GE gross efficiency, $\dot{V}E$ pulmonary ventilation, $\dot{V}O_2$ oxygen uptake, $\dot{V}CO_2$ carbon dioxide output, $\dot{V}E/\dot{V}O_2$ ventilatory equivalent ratio for oxygen, $\dot{V}E/\dot{V}CO_2$ ventilatory equivalent ratio for carbon dioxide, RER respiratory exchange ratio (*n* = 10)

* Significantly different from the pre-test session (*P* < 0.05)

Table 3 Changes in the metabolic variables measured during level running at 9 km h⁻¹ before (pre-) and after (post-) the MUM (*n* = 7)

Variable	Pre-			Post-			% Change	ES	±90 % CI
	Mean	SD	Range	Mean	SD	Range			
C_r (J m ⁻¹ kg ⁻¹)	4.6	0.9	3.7–5.8	4.5	0.8	3.2–5.6	-2.4	-0.13 (trivial)	0.25
$\dot{V}E$ (L min ⁻¹)	66.3	7.5	56.9–75.5	78.9*	14.0	62.0–107.9	+11.8	0.98 (moderate)	0.71
$\dot{V}O_2$ (L min ⁻¹)	2.2	0.3	1.8–2.7	2.2	0.3	1.9–2.7	+2.4	0.12 (trivial)	0.29
$\dot{V}CO_2$ (L min ⁻¹)	2.1	0.3	1.7–2.5	2.1	0.4	1.7–2.8	-1.2	0.06 (trivial)	0.42
$\dot{V}E/\dot{V}O_2$	30.6	3.2	25.7–35.3	35.8*	5.8	28.3–42.1	+17.2	0.97 (moderate)	0.60
$\dot{V}E/\dot{V}CO_2$	31.7	3.1	27.3–35.5	38.7*	5.8	30.8–46.6	+21.7	1.32 (large)	0.44
RER	0.96	0.03	0.93–1.00	0.92	0.09	0.91–1.00	-4.0	0.55 (small)	0.85

C_r energy cost of flat running, $\dot{V}E$ pulmonary ventilation, $\dot{V}O_2$ oxygen uptake, $\dot{V}CO_2$ carbon dioxide output, $\dot{V}E/\dot{V}O_2$ ventilatory equivalent ratio for oxygen, $\dot{V}E/\dot{V}CO_2$ ventilatory equivalent ratio for carbon dioxide, RER respiratory exchange ratio (*n* = 7)

* Significantly different from the pre-test session (*P* < 0.05)

Table 4 Changes in the metabolic variables measured during running at 6 km h⁻¹ at an inclination of +15 % (9°) before (pre-) and after (post-) the MUM (*n* = 10)

Variable	Pre-			Post-			% Change	ES	±90 % CI
	Mean	SD	Range	Mean	SD	Range			
C_r (J m ⁻¹ kg ⁻¹)	4.6	0.5	3.8–5.7	3.9*	0.6	3.1–4.8	-13.8	-1.0 (moderate)	0.48
\dot{W}_{vert} (W kg ⁻¹)	0.21	0.01	0.19–0.23	0.21	0.02	0.16–0.23	+0.1	+0.01 (trivial)	0.19
$\dot{V}E$ (L min ⁻¹)	93.6	14.6	80.0–130.4	109.6*	16.2	89.7–137.6	+17.9	+0.94 (moderate)	0.45
$\dot{V}O_2$ (L min ⁻¹)	3.1	0.3	2.5–3.7	2.8	0.3	2.4–3.2	-7.5	-0.70 (moderate)	0.45
$\dot{V}CO_2$ (L min ⁻¹)	3.1	0.4	2.5–4.1	2.9	0.4	2.3–3.4	-7.3	-0.51 (small)	0.40
$\dot{V}E/\dot{V}O_2$	30.6	3.2	25.5–35.1	37.3*	8.5	23.3–50.6	+21.6	+0.94 (large)	0.62
$\dot{V}E/\dot{V}CO_2$	30.4	3.0	25.1–33.8	39.2*	5.8	28.0–46.3	+29.2	+1.75 (large)	0.52
RER	1.00	0.05	0.94–1.10	1.00	0.09	0.88–1.10	-0.9	-0.10 (trivial)	0.32

C_r energy cost of uphill running, \dot{W}_{vert} mechanical work rate, $\dot{V}E$ pulmonary ventilation, $\dot{V}O_2$ oxygen uptake, $\dot{V}CO_2$ carbon dioxide output, $\dot{V}E/\dot{V}O_2$ ventilatory equivalent ratio for oxygen, $\dot{V}E/\dot{V}CO_2$ ventilatory equivalent ratio for carbon dioxide, RER respiratory exchange ratio (*n* = 10)

* Significantly different from the pre-test session (*P* < 0.05)

Table 5 Changes in the kinematics data measured during flat running at 9 km h⁻¹ before (pre-) and after (post-) the MUM (*n* = 7)

Variable	Pre-			Post-			% Change	ES	±90 % CI
	Mean	SD	Range	Mean	SD	Range			
<i>t_c</i> (s)	0.319	0.044	0.636–0.765	0.327	0.028	0.655–0.773	+3.4	+0.24 (small)	0.75
DF (%)	44.9	3.9	39.3–51.6	45.9	4.2	39.2–49.7	+2.8	+0.23 (small)	0.78
<i>t_c⁻¹</i> (s ⁻¹)	3.17	0.34	2.75–3.65	3.07	0.26	2.67–3.41	-2.2	-0.27 (small)	0.77
<i>t_s</i> (s)	0.392	0.037	0.341–0.458	0.388	0.046	0.341–0.471	-0.9	-0.09 (trivial)	0.52
CT (s)	0.711	0.044	0.636–0.765	0.715	0.043	0.655–0.773	+0.6	+0.08 (trivial)	0.32
FQ (Hz)	1.41	0.09	1.31–1.58	1.40	0.09	1.29–1.53	-0.5	-0.08 (trivial)	0.33
SL (m)	1.78	0.11	1.59–1.91	1.9	0.11	1.64–1.93	-0.6	-0.08 (trivial)	0.32
IC									
θ_T (°)	105	2	103–109	107	3	100–110	+0.8	+0.26 (small)	0.86
θ_L (°)	94	1	91–96	93	2	91–96	-1.0	-0.59 (small)	0.88
θ_F (°)	149	4	141–156	155	5	150–164	+4.6	+0.86 (moderate)	0.54
θ_K (°)	149	4	141–156	147	5	138–153	-1.1	-0.33 (small)	0.78
θ_A (°)	196	6	187–202	196	7	185–205	+0.1	+0.03 (trivial)	0.43
EC									
θ_T (°)	74	4	69–79	74	3	69–79	+0.3	+0.05 (trivial)	0.57
θ_L (°)	52	3	48–55	48	5	44–56	-6.0	-0.64 (moderate)	0.50
θ_F (°)	88	2	84–90	90	4	83–95	+3.0	+0.64 (moderate)	0.94
θ_K (°)	158	5	154–165	155	8	146–164	-2.1	-0.43 (small)	0.57
θ_A (°)	118	5	98–126	126	4	118–130	+6.8	+0.61 (moderate)	0.90

IC initial contact, EC end contact, *t_c* contact time, DF duty factor, *t_c⁻¹* rate of force application, *t_s* swing time, CT cycle time, FQ step frequency, SL stride length, θ_T thigh angle, θ_L shank angle, θ_F foot angle, θ_K knee angle, θ_A ankle angle (*n* = 7)

by 4.4 % (*t* = -4.6, *P* = 0.001, ES = 0.70 ± 0.28) and θ_A decreased by 4.7 % (*t* = 4.7, *P* = 0.001, ES = -1.30 ± 0.60) at the initial contact, whereas, at the end of contact, θ_L decreased by 10.0 % (*t* = 2.8, *P* = 0.019, ES = -1.05 ± 0.67) and θ_A by 3.5 % (*t* = 4.0, *P* = 0.003, ES = -1.13 ± 0.51).

Relationships between energy costs and kinematic variables

There were significant correlations only between uphill *C_r* and *t_c* [*r* = -0.63 ± 0.14 (90 % CI), *P* = 0.05], *t_c⁻¹* (*r* = 0.68 ± 0.10, *P* = 0.03) and \dot{W}_{vert} (*r* = 0.76 ± 0.10, *P* = 0.01). No significant correlation was found between the percentage changes in the variables and the performance time.

Discussion

This study sought to analyze the effect of an extreme mountain ultra-marathon on both the energy cost of three types of locomotion (cycling, level and uphill running) and running kinematics in two groups of 10 and 7 experienced ultra-marathon runners. The data show that uphill *C_r* decreased with fatigue, while *C_r* during level running and

C_{cycl} did not change. During uphill running, the decrease in *C_r* was associated with significant changes in several running kinematic variables.

Energy cost

The aim of the cycling condition was to see whether there were differences in the energy cost between running and cycling. In general, cycling is not influenced by running technique or storage of elastic energy (Bijker et al. 2001). With this procedure, we were able to distinguish between muscular- and technique-related changes in energy cost. We observed no changes in *C_{cycl}* (0.08 %) between pre- and post- (Table 2) or GE [a measure commonly used to identify the effective work in cycling (Moseley and Jeukeन्द्रup 2001)]. In contrast, uphill *C_r* significantly decreased by 13.8 % (Table 4), whereas level *C_r* remained stable (Table 3). Given that in both cycling and uphill running, the amount of concentric contractions is predominant (Bijker et al. 2002; Pringle et al. 2002), one may assume that the observed discrepancy between the specific energy costs could be entirely mode-specific and related to mechanical instead of metabolic differences.

Possible explanations for the unchanged level *C_r* include the greater eccentric contribution during level as compared with uphill running (Pringle et al. 2002). Indeed,

Table 6 Changes in the kinematics data measured during running at 6 km h⁻¹ at an inclination of +15 % (9°) before (pre-) and after (post-) the MUM (*n* = 10)

Variable	Pre-			Post-			% Change	ES	±90 % CI
	Mean	SD	Range	Mean	SD	Range			
<i>t_c</i> (s)	0.387	0.043	0.329–0.480	0.428*	0.075	0.373–0.635	+10.3	+0.61 (moderate)	0.39
DF (%)	52.1	3.5	46.9–56.6	56.2*	3.8	49.3–63.4	+8.1	+1.03 (moderate)	0.37
<i>t_c</i> ⁻¹ (s ⁻¹)	2.61	0.28	2.08–3.04	2.39*	0.31	1.58–2.68	-8.4	-0.70 (moderate)	0.34
<i>t_s</i> (s)	0.357	0.03	0.307–0.397	0.334*	0.032	0.293–0.401	-6.4	-0.68 (moderate)	0.36
CT (s)	0.742	0.053	0.681–0.848	0.759	0.096	0.647–1	+2.2	+0.21 (small)	0.38
FQ (Hz)	1.35	0.09	1.18–1.47	1.33	0.13	1–1.47	-1.8	-0.18 (trivial)	0.32
SL (m)	1.24	0.09	1.13–1.41	1.27	0.16	1.08–1.67	+2.2	+0.21 (small)	0.38
IC									
θ_T (°)	105	3	100–109	107	6	102–122	+1.9	+0.40 (small)	0.63
θ_L (°)	76	4	70–85	76	9	67–100	+0.1	+0.03 (trivial)	0.43
θ_F (°)	136	7	126–148	142*	8	134–162	+4.4	+0.70 (moderate)	0.28
θ_K (°)	151	5	141–156	149	5	138–157	-1.1	-0.32 (small)	0.57
θ_A (°)	120	5	111–126	114*	2	109–118	-4.7	-1.30 (very large)	0.60
EC									
θ_T (°)	72	3	67–76	73	4	69–80	+1.3	+0.25 (small)	0.55
θ_L (°)	47	3	44–53	42*	5	35–53	-10.0	-1.05 (moderate)	0.67
θ_F (°)	88	6	78–100	88	5	80–96	+0.3	+0.02 (trivial)	0.46
θ_K (°)	155	5	149–166	149	8	139–164	-3.6	-0.80 (moderate)	0.67
θ_A (°)	139	4	133–146	134*	4	126–138	-3.5	-1.13 (moderate)	0.51

IC initial contact, EC end contact, *t_c* contact time, DF duty factor, *t_c*⁻¹ rate of force application, *t_s* swing time, CT cycle time, FQ step frequency, SL stride length θ_T thigh angle, θ_L shank angle, θ_F foot angle, θ_K knee angle θ_A ankle angle (*n* = 10)

* Significantly different from the pre-test session (*P* < 0.05)

mechanical efficiency is higher in eccentric contraction than in concentric contraction (Komi 2000), and the return of elastic energy in the concentric phase of the stretch–shortening cycle may help in the preservation of force (de Haan et al. 1991), with lower energy expenditure (Minetti et al. 1994). Hence, the return of elastic energy in the concentric phase of the stretch–shortening cycle may also have compensated for any deficit in the force-generating capacity after the race and resulted in unchanged level-running step mechanics (Table 5) that probably did not affect the level *C_r*.

Kinematic data

Kinematic variables are known to potentially influence *C_r* (Hunter and Smith 2007). No kinematic change was noted during level running (Table 5), contrary to the changes observed during a shorter MUM where mechanical assessment was conducted at a faster overground running speed (12 km h⁻¹, 3.3 m s⁻¹) (Morin et al. 2011). A possible explanation for this discrepancy may lie in the slower speed used in the present study. Moreover, during the uphill condition, the observed DF above 50 % may indicate that the subjects had been walking. However, on qualitative

analysis of the motion of the hip marker, we noted an in-phase relationship between kinematic and potential energy of body center of mass in all subjects, indicating that they were actually running with a minimal aerial time. Running gait without an aerial phase has been called ‘grounded running’ (Rubenson et al. 2004) and it is also presented during particular forms of running, such as ‘Groucho running’ (McMahon et al. 1985), and in pre-modern humans (Schmitt 2003).

Both SF and SL are usually considered the kinematic factors that chiefly influence *C_r* (Hunter and Smith 2007). After the MUM race, we observed no changes in the SF or SL values in either the level or the uphill-running condition; therefore, the changes in *C_r* parameters in the uphill condition were unlikely to be due to changes in SF and SL.

Furthermore, during running on a positive gradient, the limb muscles perform net mechanical work to increase the body’s potential energy, while the net mechanical work required is negligible during level running as long as speed is constant (Roberts and Belliveau 2005). The increased demand for work as the gradient increases is met by an increase in power output at several joints (Roberts and Belliveau 2005). We found that there were changes in the functions at the shank, the ankle, and the

foot between the pre- and post-sessions in the uphill-running condition (Table 6) that mainly affected the ankle joint, whereas no change was detected in level running (Table 5).

During uphill running, SF did not change after the race. However, t_c increased by 10.3 % and t_s decreased by 6.4 % from pre- to post-, respectively. This was associated with an 8.1 % higher DF. An increase in t_c means a longer time to express the required propulsive force, and this may be associated with a decrease in the rate of force development. Moreover, while SF and, then, SL remained unchanged, the subjects re-organized their running mechanics toward a higher t_c , thus leading to a longer DF, indicating that the rate at which the reaction forces must be generated decreased from pre- to post-. This suggests that in the fatigue condition, the subjects were probably no longer able to generate a high rate of force development, thus increasing the propulsive force time (Siler and Martin 1991; Hayes et al. 2004).

Furthermore, the increase in t_c , DF, and the decrease in t_s are consistent with the observed modifications in the angular kinematics of the thigh, shank, and foot in both IC and EC time. Specifically, in the IC a significant decrease in θ_A by 4.7 % accompanied by a rise in θ_F by 4.4 % may suggest a loss of tolerance to impact forces during IC, in which the foot hits the ground at a greater angle and is positioned more parallel to the ground (Blickhan 1989). The significant decreases in θ_L and θ_A (10.0 and 3.5 %, respectively) during EC suggest that longer contact times occurred because of a prolonged relative duration of the push-off phase (Nicol et al. 1991a).

Relationships between energy costs and kinematic variables

We observed a significant and negative relationship between t_c and uphill C_r which, in turn, implies a proportionality between the rate of force application (t_c^{-1}) and uphill C_r . This suggests that changes in the uphill-running patterns might explain the decreased C_r observed in the fatigue condition, because C_r is also determined by the rate at which force must be generated by the muscles that support the body during the stance phase (Roberts et al. 1998). Previous studies of shorter running tasks (Cavanagh and Williams 1982; Nelson 1983; Cavanagh and Kram 1985; Hunter and Smith 2007) and ultra-long distance runs (Morin et al. 2011; Degache et al. 2013) have shown that such changes may lead to a ‘smoother’ and a more economical running style. It was noted that subjects were still capable of adjusting their uphill-running characteristics despite a decrease in the force capabilities of the main lower limb muscles likely due to muscle damage and inflammation processes (Saugy et al. 2013).

Limitations

One of the potential limitations of the present study is the objection that the gait characteristics observed on a treadmill may differ from those during overground running and affect the C_r (Nicol et al. 1991a). This is an alternative hypothesis for the observed decrease in uphill C_r . Indeed, treadmill-based analysis of running mechanics can be generalized to overground running mechanics (Riley et al. 2008) until the speed of 18 km h⁻¹ (5 m s⁻¹) (Williams 1985). Moreover, use of the treadmill ensures steady-state conditions (Riley et al. 2008) that cannot be obtained with overground running.

Perspectives and practical applications

Some of the measurements performed here would be hard to replicate in the field following an extreme mountain ultra-marathon. Nonetheless, this study presents new data on performance factors hitherto lacking in the literature for this type of extreme endurance exercise. With this study, we documented the changes in metabolic and kinematic variables in a group of runners after an extreme mountain ultra-marathon. Because of the heterogeneity of our sample and because of the paucity of data on the apparent reduction in uphill energy cost following an extreme prolonged exercise, the data reported in this study are primarily descriptive in nature. Future studies are therefore needed, with well-controlled serial measures of post-race measurements in a more homogeneous sample to determine the time-course changes of this effect.

Conclusion

We observed a decrease in uphill energy cost, as compared to energy costs in both cycling and level running, as well as an increase in t_c and DF in a group of ultra-runners who participated in this extreme mountain ultra-marathon. We presume that the decrease in the capacity of muscle force generation, as a natural consequence of an extreme mountain ultra-marathon race, induced the subjects to modify only their uphill-running step mechanics, which likely altered the relative involvement of muscle groups and/or the pattern of motor unit recruitment in these muscles. This resulted in an altered uphill-running pattern that reduced the energy cost of uphill running and likely reduced the discomfort to the lower limb muscles following such an extreme endurance event.

Acknowledgments The authors wish to thank the subjects involved in the present study for their participation, especially during the test sessions in the fatigue condition. We would also like to express our gratitude to Aurelio Marguerettaz, the Regione Autonoma della Valle

d'Aosta, the Tor de Géants® Organizing Committee, the Courmayeur Trailers, and Maurizio Capolupo. We thank also Kenneth A. Britsch for checking the manuscript for English.

References

- Abbs CR, Laursen PB (2008) Describing and understanding pacing strategies during athletic competition. *Sports Med* 38:239–252
- Bijker KE, De Groot G, Hollander AP (2001) Delta efficiencies of running and cycling. *Med Sci Sports Exerc* 33:1546–1551
- Bijker KE, de Groot G, Hollander AP (2002) Differences in leg muscle activity during running and cycling in humans. *Eur J Appl Physiol* 87:556–561
- Blickhan R (1989) The spring-mass model for running and hopping. *J Biomech* 22:1217–1227
- Brückner JC, Atchou G, Capelli C, Duvallet A, Barrault B, Jousse-lin E, Rieu M, di Prampero PE (1991) The energy cost of running increases with the distance covered. *Eur J Appl Physiol* 62:385–389
- Cappozzo A, Catani F, Croce UD, Leardini A (1995) Position and orientation in space of bones during movement: anatomical frame definition and determination. *Clin Biomech (Bristol, Avon)* 10:171–178
- Cavanagh PR, Kram R (1985) Mechanical and muscular factors affecting the efficiency of human movement. *Med Sci Sports Exerc* 17:326–331
- Cavanagh PR, Williams KR (1982) The effect of stride length variation on oxygen uptake during distance running. *Med Sci Sports Exerc* 14:30–35
- de Haan A, Lodder MAN, Sargeant AJ (1991) Influence of an active prestretch on fatigue of skeletal muscle. *Eur J Appl Physiol* 62:268–273
- Degache F, Guex K, Fourchet F, Morin JB, Millet GP, Tomazin K, Millet GY (2013) Changes in running mechanics and spring-mass behaviour induced by a 5-h hilly running bout. *J Sports Sci* 31:299–304
- di Prampero PE, Salvadego D, Fusi S, Grassi B (2009) A simple method for assessing the energy cost of running during incremental tests. *J Appl Physiol* 107:1068–1075
- Foissac MJ, Berthollet R, Seux J, Belli A, Millet GY (2008) Effects of hiking pole inertia on energy and muscular costs during uphill walking. *Med Sci Sports Exerc* 40:1117–1125
- Gimenez P, Kerhervé H, Messonnier LA, Féasson L, Millet GY (2013) Changes in the energy cost of running during a 24-h treadmill exercise. *Med Sci Sports Exerc* 45:1807–1813
- Hayes PR, Bowen SJ, Davies EJ (2004) The relationships between local muscular endurance and kinematic changes during a run to exhaustion at $v\text{VO}_2\text{max}$. *J Strength Cond Res* 18:898–903
- Higham TE, Biewener AA (2008) Integration within and between muscles during terrestrial locomotion: effects of incline and speed. *J Exp Biol* 211:2303–2316
- Hunter I, Smith GA (2007) Preferred and optimal stride frequency, stiffness and economy: changes with fatigue during a 1-h high-intensity run. *Eur J Appl Physiol* 100:653–661
- Knechtle B (2012) Ultramarathon runners: nature or nurture? *Int J Sports Physiol Perform* 7:310–312
- Komi PV (2000) Stretch-shortening cycle: a powerful model to study normal and fatigued muscle. *J Biomech* 33:1197–1206
- Kyröläinen H, Pullinen T, Candau R, Avela J, Huttunen P, Komi PV (2000) Effects of marathon running economy and kinematics. *Eur J Appl Physiol* 82:297–304
- Lazzer S, Salvadego D, Rejc E, Buglione A, Antonutto G, di Prampero PE (2012) The energetics of ultra-endurance running. *Eur J Appl Physiol* 112:1709–1715
- McMahon TA, Valiant G, Frederick EC (1985) Groucho running. *J Appl Physiol* 62:2326–2337
- Millet GP (2012) Economy is not sacrificed in ultramarathon runners. *J Appl Physiol* 113:686
- Millet GP, Millet GY (2012) Ultramarathon is an outstanding model for the study of adaptive responses to extreme load and stress. *BMC Med* 10:77
- Millet G, Lepers R, Lattier G, Martin V, Babault N, Maffiuletti N (2000) Influence of ultra-long-term fatigue on the oxygen cost of two types of locomotion. *Eur J Appl Physiol* 83:376–380
- Millet GY, Lepers R, Maffiuletti NA, Babault N, Martin V, Lattier G (2002) Alterations of neuromuscular function after an ultramarathon. *J Appl Physiol* 92:486–492
- Millet GP, Vleck VE, Bentley DJ (2009a) Physiological differences between cycling and running. Lessons from triathletes. *Sports Med* 39:179–206
- Millet GY, Morin JB, Degache F, Edouard P, Feasson L, Verney J, Oullion R (2009b) Running from Paris to Beijing: biomechanical and physiological consequences. *Eur J Appl Physiol* 107:731–738
- Millet GY, Banfi JC, Kerherve H, Morin JB, Vincent L, Estrade C, Geysant A, Feasson L (2011a) Physiological and biological factors associated with a 24 h treadmill ultra-marathon performance. *Scand J Med Sci Sports* 21:54–61
- Millet GY, Tomazin K, Verges S, Vincent C, Bonnefoy R, Boisson RC, Gergele L, Feasson L, Martin V (2011b) Neuromuscular consequences of an extreme mountain ultra-marathon. *PLoS One* 6:e17059
- Millet GY, Hoffman MD, Morin JB (2012) Sacrificing economy to improve running performance—a reality in the ultramarathon? *J Appl Physiol* 113:507–509
- Minetti AE, Ardigò LP, Saibene F (1994) Mechanical determinants of the minimum energy cost of gradient running in humans. *J Exp Biol* 195:211–225
- Minetti AE, Moia C, Roi GS, Susta D, Ferretti G (2002) Energy cost of walking and running at extreme uphill and downhill slopes. *J Appl Physiol* 93:1039–1046
- Morin JB, Tomazin K, Edouard P, Millet GY (2011) Changes in running mechanics and spring-mass behavior induced by a mountain ultra-marathon race. *J Biomech* 44:1104–1107
- Moseley L, Jeukendrup AE (2001) The reliability of cycling efficiency. *Med Sci Sports Exerc* 33:621–627
- Nelson WL (1983) Physical principles for economies of skilled movements. *Biol Cybern* 46:135–147
- Nicol C, Komi PV, Marconnet P (1991a) Effects of marathon fatigue on running kinematics and economy. *Scand J Med Sci Sports* 1:195–204
- Nicol C, Komi PV, Marconnet P (1991b) Fatigue effects of marathon running on neuromuscular performance. Changes in force, integrated electromyographic activity and endurance capacity. *Scand J Med Sci Sports* 1:18–24
- Padulo J, Powell D, Milia R, Ardigò LP (2013) A paradigm of uphill running. *PLoS One* 8:e69006
- Pringle JSM, Carter H, Doust JH, Jones AM (2002) Oxygen uptake kinetics during horizontal and uphill treadmill running in humans. *Eur J Appl Physiol* 88:163–169
- Riley PO, Dicharry J, Franz J, Della Croce U, Wilder RP, Kerrigan DC (2008) A kinematics and kinetic comparison of overground and treadmill running. *Med Sci Sports Exerc* 40:1093–1100
- Roberts TJ, Belliveau RA (2005) Sources of mechanical power for uphill running in humans. *J Exp Biol* 208:1963–1970
- Roberts TJ, Kram R, Weyand PG, Taylor CR (1998) Energetics of bipedal running. I. Metabolic cost of generating force. *J Exp Biol* 201:2745–2751
- Rubenson J, Heliam DB, Lloyd DG, Fournier PA (2004) Gait selection in the ostrich: mechanical and metabolic characteristics of

- walking and running with and without an aerial phase. *Proc Biol Sci* 271:1091–1099
- Saugy J, Place N, Millet GY, Degache F, Schena F, Millet GP (2013) Alterations of neuromuscular function after the world's most challenging mountain ultra-marathon. *PLoS One* 8:e65596
- Schmitt D (2003) Insights into the evolution of human bipedalism from experimental studies of humans and other primates. *J Exp Biol* 206:1437–1448
- Schobersberger W, Wirleitner B, Puschendorf B, Koller A, Villiger B, Frey W, Mair J (1996) Influence of an ultramarathon race at moderate altitude on coagulation and fibrinolysis. *Fibrinolysis* 10:37–42
- Siler WL, Martin PE (1991) Changes in running pattern during a treadmill run to volitional exhaustion: fast versus slower runners. *Int J Sport Biomech* 7:12–28
- Snyder KL, Farley CT (2011) Energetically optimal stride frequency in running: the effects of incline and decline. *J Exp Biol* 214:2089–2095
- Snyder KL, Kram R, Gottschall JS (2012) The role of elastic energy storage and recovery in downhill and uphill running. *J Exp Biol* 215:2283–2287
- Taylor CR, Caldwell SL, Rowntree VJ (1972) Running up and down hills: some consequences of size. *Science* 178:1096–1097
- Vitiello D, Rupp T, Bussière JL, Robach P, Polge A, Millet GY, Nottin S (2013) Myocardial damages and left and right ventricular strains after an extreme mountain ultra-long duration exercise. *Int J Cardiol* 165:391–392
- Williams KR (1985) Biomechanics of running. *Exerc Sport Sci Rev* 13:389–441
- Winter DA (2009) The biomechanics and motor control of human gait: normal, elderly and pathological, 4th edn. Wiley, Hoboken