



Original research

Energetically optimal stride frequency is maintained with fatigue in trained ultramarathon runners

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ABSTRACT

Objectives: At a given running speed, humans naturally endeavor to achieve an optimal stride frequency that minimizes metabolic cost. Research has suggested that runners select this near optimal stride frequency in some process of self-optimization even during fatiguing tasks up to 1-h of high-intensity running. Here, we studied whether runners demonstrate a similar self-optimizing capability after an ultramarathon of 6 h.

Design: Controlled pre–post study.

Method: We collected temporal stride kinematics and metabolic data in nine (experimental group) male runners before and after 6 h of running and in six (control group) male ultramarathon runners who did not run, but stayed awake and performed normal, daily physical activities avoiding strenuous exercises over the 6-h period. For each participant, preferred and optimal stride frequencies were measured, where stride frequency was systematically varied above and below PSF ($\pm 4\%$ and $\pm 8\%$).

Results: Preferred and optimal stride frequencies across time and group showed no significant differences ($p \geq 0.276$). Furthermore, neither the overall relationship between metabolic cost and stride frequency, nor the energetically optimal stride frequency changed substantially after several hours of running.

Conclusions: Similar dynamics of stride frequency adjustments in the experimental group occurred as those found in a non-fatigued state. This suggests that after an ultramarathon of 6 h, runners were still able to optimize their gait, and automatically adjust it in order to converge on the energetically optimal gait.

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Practical implications

- After a fatiguing task consisting of an ultramarathon of 6 h, runners were still able to maintain similar stride frequencies to those found in a non-fatigued state.
- Runners can still optimize their gait, suggesting that the same control strategies underlying gait parameter selection in a non-fatiguing state remain in place.
- It is possible that runners are able to optimize their running gait with some processes of self-optimization and automatically adjust it to preserve the energetically optimal one.

1. Introduction

An important principle underlying the physiological basis of human locomotion is that for a given speed of locomotion, humans choose the gait that minimizes mass-specific metabolic cost.¹ Within running gaits, runners tend to modulate their speed primarily by choosing the stride frequency (SF) that minimizes their energy use.² In terms of endurance running speeds, this SF [known as preferred SF (PSF)], is usually close to the optimal SF (OSF) that minimizes mass-specific metabolic cost. In this case, either an increase or a decrease in SF would lead to a parabolic relationship with metabolic cost.^{3,4} That is, the rate of metabolic energy consumption is greater at frequencies faster or slower than the PSF. Different explanations have been proposed to explain why metabolic cost is minimized at PSF, such as the maximization of

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elastic energy storage in the lower limbs⁵ and the biomechanical and energetic trade-off between external and internal work.⁶ However, none have been conclusively proven. Despite this, research documents runners' tendency to select a near OSF because (i) the kinematic patterns (such as SF) have a direct impact on the metabolic cost at a given running speed,⁷ and/or (ii) some processes of subconscious self-optimization are in place.^{3,4} Interestingly, it seems that this latter point is present even during fatiguing running tasks of up to a 1-h high-intensity run.⁸

Fatigue in ultramarathon running is a highly complex phenomenon, acting at numerous physiological and biomechanical sites and translating to mechanical changes. After ultramarathons, participants experienced strength loss and increased levels of inflammatory and muscle damage markers, as well as structural and functional alterations.^{9,10} This ultimately reduces maximal force-generating capacity and the ability for muscle stretch; and also produces some delay between the first (eccentric) and the second (concentric) action in the stretch-shortening cycle. Furthermore, these changes are likely the result of modified stiffness properties of the leg system.^{11–13} Therefore, the literature thus far has observed that the muscular and mechanical properties of the leg muscles decrease after several hours of running,^{12,13} and consequently, participants increase their SF for a given and absolute running speed.^{11,14,15} This increased SF would act as a compensatory biomechanical adjustment to generate a “smoother” and “safer” running style, a running strategy to limit the overall loading experienced at each running step, and therefore minimize the damage to the lower limb tissue and the extent of muscular fatigue.¹⁶ According to the parabolic relationship between SF and metabolic cost previously described, the rate of metabolic energy consumption should be greater if a new SF is adopted.¹⁷

Ultramarathon running (*i.e.* any distance greater than that of a marathon), constitutes an interesting paradigm to investigate this possibility. Indeed, this type of exercise is challenging for the homeostasis, energetic, and muscular systems and therefore may be able to trigger adaptive responses above the preferred condition. Therefore, in the present study we determine whether runners demonstrate a similar (or different) self-optimizing capability after an ultramarathon of 6 h.

2. Methods

Fifteen runners participated in the study. Nine (8M/1F, age 33 ± 13 yr, height 177 ± 9 cm, body mass 71 ± 7 kg, mean \pm SD) took part in the 6-h run and served as the experimental group (EXP). Data collection was also performed on six runners (5M/1F, age 33 ± 9 yr, height 176 ± 10 cm, body mass 68 ± 4 kg) who served as the control group (CON). Both EXP and CON were physically fit and experienced ultramarathon runners, having already run a race longer than 6 h or greater than 50 km. CON did not run, but stayed awake over the 6-h period and performed normal, daily physical activities avoiding strenuous exercises. None of them had any lower extremity injuries within the last six months prior to their participation that might have otherwise compromised their gait. The study was approved by the local institute's research ethics committee and written informed consent was obtained from each participant.

Each participant completed one preliminary session and two data collection sessions. Preliminary sessions took place 2–3 weeks before the experiment, where participants performed a maximal test on a motorized treadmill. They also performed a familiarization consisting of countermovement-jumps (CMJs) practice with an emphasis on the speed of jump. The first data collection session was performed 24 h preceding the ultramarathon of 6 h (PRE). Participants were asked to refrain from intense physical activity in the 24 h preceding PRE. They were also asked to consume their last meal at least 3 h before PRE and to refrain from consuming drinks

containing caffeine or alcohol for at least 12 h preceding PRE. During the first collection session, participants performed CMJ-testing sessions followed by five stages of 5-min running, interspersed by 5-min rest periods. For the first running stage, each participant ran at 3 m s^{-1} without any instructions so that we could determine her/his PSF. Subsequently, each participant was instructed to run at 3 m s^{-1} and in synchronization with a computer-based metronome randomly set to four different SFs (*i.e.* at $\pm 4\%$ and $\pm 8\%$ of PSF).⁸ The second data collection session was performed immediately after the 6-h run (POST) in the same laboratory and location of PRE. Time duration between the end of the 6-h run and starting the POST testing procedures was <5 min. During the second data collection run, participants completed the same protocol described above, with a new randomization of altered SFs.

The maximal test on a motorized treadmill (Gymrol S2500, HEF Tecmachine, Andrézieux-Bouthéon, France) aimed at determining the gas exchange threshold (GET) and the maximal oxygen uptake ($\dot{V} \text{ O}_{2\text{max}}$). After a warm-up of 10 min at 3 m s^{-1} , the initial velocity was set at 3.6 m s^{-1} with the first stage lasting 2 min. Then, the test consisted of a maximal incremental test where the speed was progressively increased by 0.28 m s^{-1} every 2 min until exhaustion. Breath-by-breath pulmonary gas exchange and ventilation were continuously measured via metabolic cart (Metalyzer 3B-R3 system; Cortex Biophysics, Leipzig, Germany). Calibration was performed before each test according to manufacturer instructions. GET was visually determined according to standardised procedures described elsewhere.¹⁸ $\dot{V} \text{ O}_{2\text{max}}$ was defined according to primary¹⁹ or secondary²⁰ criteria.

At PRE and POST, participants performed 3 CMJ trials with 30 s rest between. The maximum jump height achieved and the vertical peak force normalized per the participants' body mass (N kg^{-1}) were measured using a portable force platform (Quattro-Jump, Kistler, Winterthur, Switzerland) at a sampling rate of 500 Hz according to standardized procedures. The average values of the 3 CMJ trials were used in the subsequent statistical analysis. CMJ is a suitable method to assess fatigue-induced changes in the neuromuscular function, with averaged values deemed more sensitive in monitoring the neuromuscular status.²¹

The running exercise started between 8:00 AM and 12:00 PM and ended 6 h later. Participants ran on an 11.5-km loop (with an elevation change of 550 m) that was designed around the location of the laboratory at a freely chosen pace, with the aim to cover the longest distance possible. As the running speed could be modified at any time during the 6-h period (such as in a normal race), small loops were added close to the laboratory to be sure the runners ended the 6-h exercise as close as possible to there. Thus, the time between the end of the running task and POST evaluations was kept constant for every runner.

The metabolic cost of running (Cr) at different SFs was measured using the metabolic cart (Metalyzer 3B-R3 system) in a closed room with constant temperature and humidity. The first 4 min of each 5-min measurement were not used in the analysis in order to obtain 1 min at a flat, steady-state $\dot{V} \text{ O}_2$ plateau. Cr was determined according to standardized procedures described elsewhere^{15,22} and expressed in $\text{J kg}^{-1} \text{ m}^{-1}$.¹⁷

OSF was determined by means of a treadmill-level high-density photoelectric cells system (Optogait, Microgate, Bolzano, Italy) as described elsewhere.^{15,22} To allow for any asymmetric increase in Cr on either side of the optimum, we first determined an *n*-th order polynomial by using the least-squares method with SF as the independent variable and Cr as the dependent variable. OSF has been shown to be within the range of either a second-⁴ or third-³ order polynomial regression; therefore, the polynomial regression model that minimized the variance between the values estimated from the polynomial and the expected values from the dataset was deemed appropriate for subsequent analysis. For a second-order poly-

mial regression, the optimum was then calculated as the minimum value of this function. For a third-order polynomial regression, the optimum was calculated by finding the zero of the derivative of the third-order function for which the second derivative was positive. Custom-written Matlab code (The MathWorks Inc., Natick, MA) was used to analyze optimum data.

Results are given in the text as means \pm SD and in figures as means \pm SEM. Generalized estimating equations (GEE) were employed to account for the unbalanced and small participant numbers and to obtain unbiased estimates as well as to take into account the correlation between repeated measurements in CMJs, net metabolic cost and stride frequency parameters.²³ Particularly, GEE was employed to longitudinally analyze whether SF affected Cr similarly PRE and POST the 6-h running bout, as well as longitudinal differences in PSF versus OSF. When significant main effects were observed, Bonferroni's test was used for *post-hoc* analysis. The magnitude of the changes was assessed using Cohen's effect size d (d) with 95% confidence interval (CI). D values of 0.2, 0.5, and above 0.8 were considered *small*, *medium*, and *large*, respectively.²⁴ Statistical analyses were performed using IBMTM SPSSTM Statistics (version 24.0.0.1, IBM Corp., Somers, New York, NY). Statistical significance was set at $p < 0.05$.

3. Results

During the ultramarathon of 6 h, the effective running distance in EXP was 44.3 ± 2.8 km (with 2276 ± 487 m of positive elevation gain). Mean \pm SD $\dot{V}O_{2\max}$ values were 67.3 ± 11.5 and 66.2 ± 10.2 mL O_2 kg^{-1} min^{-1} for EXP and CON, respectively. While, mean \pm SD of GET values were 44.5 ± 6.0 and 43.6 ± 2.9 mL O_2 kg^{-1} min^{-1} for EXP and CON, respectively. Both at PRE and POST, all the participants' $\dot{V}O_2$ values during the running condition at PSF were below the corresponding values at GET.

CMJ parameters presented significant group \times time interactions both for maximum jump height [χ^2 (1) = 32.604, $p < 0.001$] and for vertical peak force [χ^2 (1) = 11.909, $p = 0.001$]. In CON, CMJ performances did not decline between PRE and POST both when expressed as maximum jump height achieved (23.4 ± 6.8 and 23.8 ± 6.7 cm, $p = 0.321$, $d \pm 95\%CI$: 0.05 ± 0.13) and vertical peak force (21.3 ± 2.6 and 21.2 ± 2.8 N kg^{-1} , $p = 0.591$, d : 0.04 ± 0.19). In EXP, a 10.9% and a 7.4% reduction in the maximum jump height achieved (26.3 ± 6.0 and 23.3 ± 5.0 cm, $p < 0.001$, d : 0.49 ± 0.18) and in the vertical peak force (20.9 ± 3.5 and 19.3 ± 3.3 N kg^{-1} , $p < 0.001$, d : 0.41 ± 0.23) were observed between PRE and POST, respectively.

Both EXP and CON showed the lowest Cr at the PSF, while either faster or slower SFs lead to increased Cr (Table 1; Fig. 1 top panel). By using a slow SF, equal to 92% PSF, EXP and CON increased metabolic cost at PRE and POST by 8.5% and 9% compared with the PSF, respectively. By using a fast SF, equal to 108% PSF, EXP and CON increased metabolic cost at PRE and POST by 6.5% and 5% compared with the PSF, respectively (Fig. 1, bottom panel). No significant group \times time interaction was observed for PSF [χ^2 (1) = 0.556, $p = 0.456$] and OSF [χ^2 (1) = 0.176, $p = 0.675$]. Furthermore, there was no group \times SF \times interaction [χ^2 (1) = 0.067,

$p = 0.796$], implying that Cr showed similar dependence on SF across the two time periods.

4. Discussion

In the present study, we examined whether a fatiguing ultramarathon of 6 h may have introduced a potentially perturbing factor in the runners' self-optimizing capability or not. Results from CMJ tests showed fatigue-induced changes in the neuromuscular function of the lower-limbs (that may have induced significant changes of stride frequency and metabolic cost). However, neither the pattern of SF versus metabolic cost, nor the OSF significantly changed with fatigue after the ultramarathon of 6 h.

In both EXP and CON, OSF was similar to PSF before the ultramarathon of 6 h, confirming previous findings that showed self-optimization in non-fatigued conditions.^{3,4} A number of plausible explanations have been put forth to explain this self-optimization process. Running is a bouncing gait in which elastic energy is stored in muscles, tendons and ligaments of the lower limbs during the first half of stance and then released during the second half of stance. If OSFs maximize the contribution of elastic energy exchange relative to total work, then muscles can perform less mechanical work and expend less metabolic energy.⁵ However, factors other than elastic energy storage also contribute to OSF; variations in SF affected the metabolic cost less on inclined versus flat surfaces because the elastic energy storage is reduced on slopes.³ Another mechanism to be considered is the biomechanical and energetic trade-offs of producing external work versus internal work. In running, the chosen SF tends to be below the symmetrical bouncing frequency that minimizes external work, in order to lower the internal work cost of accelerating and decelerating the limbs at higher frequencies.⁶ Further, OSF is a function of minimizing the average force produced by lower limb muscles per step (which is greater at lower SFs) and minimizing limb stiffness (which is greater at higher SFs).²⁵

The lack of fatigue-induced changes in SF for a given running speed is contrary to findings in ultramarathon studies exploring the relation between SF and fatigue.^{11–15} However, these studies recorded SF at a given speed using different running speeds compared to the present study. Conversely, other studies revealed no change in SF after ultramarathons.^{26,27} However, these studies recorded SF at the participants' free running speed implying that some potential real changes may have then been hidden because of differences between participants' running at different speeds. Taken together, it is impossible to ascertain that results would have been the same if the running speeds were equal for all studies. Here, we reason that SF was unrelated to the ultramarathon because of the unique population of runners studied. Given their high-performance capacity (as evidenced by high $\dot{V}O_{2\max}$ values), and the fact that the most economical runners are also the one who present greatest values of SFs,^{28,29} it may be that our participants' stride characteristics have been more fatigue-resistant than, for example, those studied before (recreational or even high performing ultramarathon runners). Consequently, findings simi-

Table 1

Mean (SD) values for the net metabolic cost at a speed of 3 m s^{-1} at each stride frequency in the experimental (EXP, n=9) and control (CON, n=6) group.

Stride frequency	EXP net metabolic cost (J kg^{-1} m^{-1})		CON net metabolic cost (J kg^{-1} m^{-1})		Group \times time interaction (p level)
	PRE	POST	PRE	POST	
92% of PSF	3.86 (0.45)	3.72 (0.38)	3.80 (0.33)	3.73 (0.26)	0.575
96% of PSF	3.68 (0.39)	3.60 (0.33)	3.64 (0.32)	3.59 (0.22)	0.759
PSF	3.53 (0.34)	3.48 (0.31)	3.50 (0.25)	3.42 (0.21)	0.658
104% of PSF	3.64 (0.43)	3.57 (0.37)	3.58 (0.26)	3.48 (0.20)	0.648
108% of PSF	3.82 (0.57)	3.66 (0.39)	3.65 (0.23)	3.63 (0.19)	0.268

PSF, preferred stride frequency.

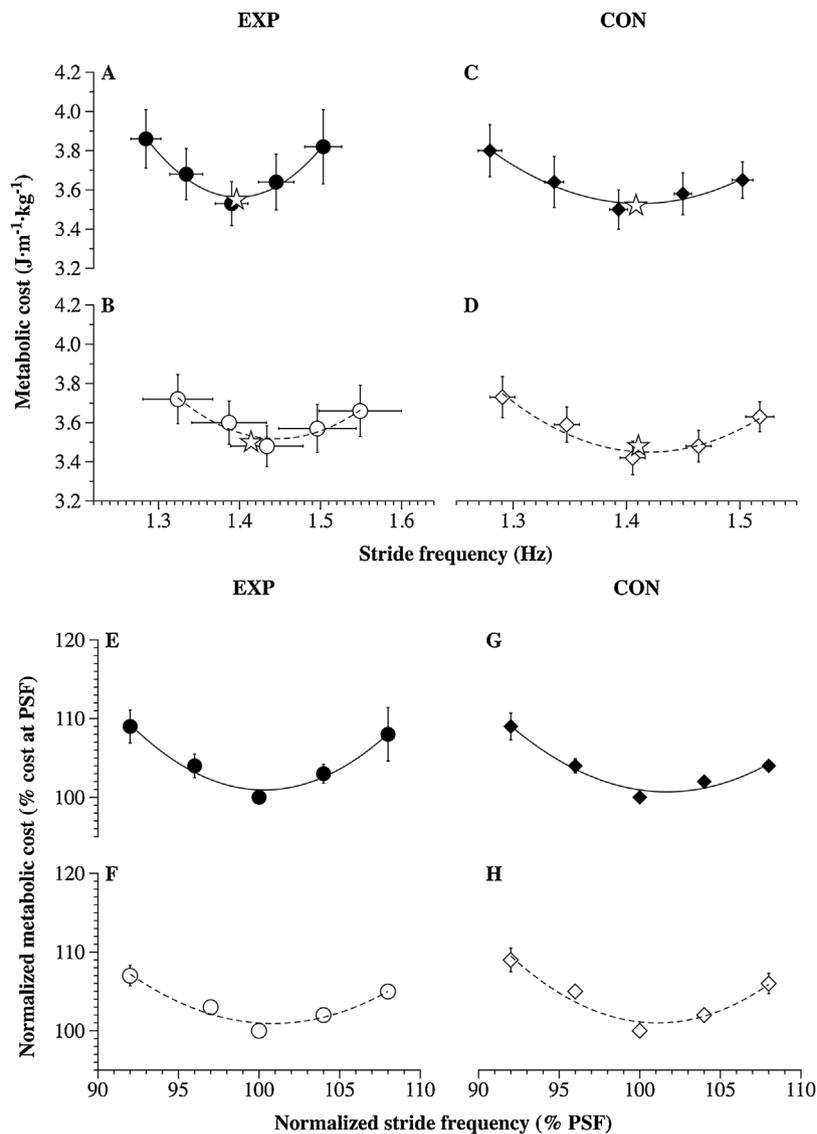


Fig. 1. Top panel. The relationship between stride frequency and metabolic cost at a speed of 3 m s^{-1} in the experimental (EXP, $n=9$) and control (CON, $n=6$) group before (A and C) and after (B and D) a 6-h running bout. Bottom panel. Metabolic cost and stride frequency values are given as a percentage of cost at the preferred stride frequency (PSF) and as percentage of PSF, respectively. The points represent the mean for EXP and CON and the error bars are SEM. Stars represent mean optimal stride frequencies. These were calculated by performing regression analysis (see ‘Establishing optimal stride frequency’ section). All the regression lines are a third-order polynomial fit to the mean data, with $r \geq 0.96$.

lar values of SFs in EXP to those found in a non-fatigued state would suggest that the same control strategies underlying gait parameter selection were in place both before and after several hours of running, with the aim of minimizing the metabolic cost. This suggests that the metabolic cost is key in the selection of SF in human running, thereby serving as an optimality criterion. This observation is also based on the fact that before and after the ultramarathon of 6 h EXP presented SFs of 1.4 Hz (i.e. $85\text{ strides min}^{-1}$), which are close to the natural (resonance) frequency of the human body during running at submaximal speeds.⁵ Running at these frequencies would maximize step-to-step energy conservation, with optimal storage of energy in the muscular tendon system during landing and subsequent release during push off.³⁰

In interpreting the results of the current study, the method of OSF measurement must be considered. The data were collected manipulating SF by $\pm 4\%$ and $\pm 8\%$ of PSF. These manipulations may have been too close to the PSF to fully appreciate significant Cr changes. However, literature suggests that alterations as minor as $\pm 3\%$ and $\pm 6\%$ already result in detrimental effects upon Cr.⁷ Further, these values were selected to provide a wide enough range of

SFs to allow for calculation of the OSF, but constrained near their PSF so that their effort could be sustained for the full 5-min trials.

5. Conclusion

Our results are a strong test of generality because our current knowledge about fatigue-related self-optimization has been limited to tasks up to 1-h of high-intensity running.⁸ Here we expanded that finding, showing that after an ultramarathon of 6 h runners were still able to optimize their running gait and automatically adjust it to the novel circumstances (i.e. fatigue) in order to converge on the energetically optimal gait.

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