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Performance factors of prolonged running: a particular focus on running economy and fatigue

Frederic Sabater Pastor

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**PERFORMANCE FACTORS OF PROLONGED RUNNING:
A PARTICULAR FOCUS ON RUNNING ECONOMY
AND FATIGUE**

**FACTEURS DE LA PERFORMANCE EN COURSE À PIED :
ROLE DE L'ECONOMIE DE COURSE ET DE LA FATIGUE**

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Abstract

The objectives of this thesis were to investigate the performance determinants of trail running, and to evaluate the changes in running economy following prolonged endurance running exercise. First, we tested elite road and trail runners for differences in performance factors. Our results showed that elite trail runners are stronger than road runners, but they have greater cost of running when running on flat ground. In the second study, we evaluated the performance factors that predicted performance in trail running races of different distances, ranging from 40 to 170 km. We found that maximal aerobic capacity was a determinant factor of performance for races up to 100 km. Performance in shorter races, up to approximately 55 km, was also predicted by lipid utilization at slow speed, while performance in the 100 km race was also predicted by maximal strength and body fat percentage. The most important factors of performance for races longer than 100 km are still debated. We also tested the effects of trail running race distance on cost of locomotion, finding that cost of running increased after races up to 55 km, but not after races of 100-170 km. Finally, we tested the effects of two different exercise modalities, cycling and running, on cost of locomotion, after 3 hours of intensity-matched exercise. Cost of locomotion increased more following cycling than running, and the change in cost of locomotion was related to changes in cadence and loss of force production capacity.

Résumé

Les objectifs de cette thèse étaient d'étudier les déterminants de la performance de la course de trail, et d'évaluer les modifications d'économie de course (RE) après un exercice de course d'endurance prolongé. Nous avons dans un premier temps étudié les facteurs de la performance chez des coureurs sur route vs des coureurs de trail élite. Nos résultats ont montré que les coureurs de trail élite sont plus forts que les coureurs sur route, mais ont une moins bonne RE lorsqu'ils courent à plat. Dans la deuxième étude, nous avons évalué les facteurs permettant de prédire les performances en courses de trail de différentes distances, allant de 40 à 170 km. Nous avons constaté que la puissance maximale aérobie était un facteur déterminant de la performance pour les courses jusqu'à 100 km. La performance dans les courses plus courtes, jusqu'à environ 55 km, était également prédite par l'utilisation des lipides à faible vitesse, tandis que la performance sur les courses de 100 km était prédite par la force maximale des extenseurs du genou et le pourcentage de masse grasse. Les facteurs les plus importants pour la performance dans les courses de plus de 100 km sont encore débattus. Dans une 3^{ème} étude, nous avons testé les effets de la distance des courses de trail sur RE. Nous avons constaté que RE se dégradait après des courses allant jusqu'à 55 km, mais pas lors des courses de 100 à 170 km. Enfin, dans une 4^{ème} étude, nous avons testé les effets de deux modalités d'exercice différentes, le vélo et la course à pied, sur le coût de la locomotion, après 3 heures d'exercice à même intensité. Le coût de la locomotion a augmenté davantage après le cyclisme qu'après la course à pied, et le changement du coût de la locomotion en cyclisme était lié aux changements de cadence et à la perte des capacités de production de force.

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List of abbreviations

%Fat10	Percentage of energy derived from lipids while running at 10 km/h
[La-]	Blood Lactate Concentration
ANOVA	Analysis of Variance
BMI	Body Mass Index
CHO	Carbohydrate
C_L	Cost of Locomotion
O_2C	Oxygen Cost of Running
Cr	Energy Cost of Running
Cr-breath	Energy Cost of Running Minus Cost of Breathing
CT	Contact Time
D+	Vertical gain accumulated
DF	Duty Factor
F_0	Theoretical maximal force derived from the force-velocity profile
FT	Flight Time
GET	Gas Exchange Threshold
HR	Heart Rate
HRmax	Maximal Heart Rate
HRR	Heart Rate Reserve
ISF	International Skyrunning Federation
ITRA	International Trail Running Association
KE	Knee extensors
KF	Knee flexors
Kleg	Leg Stiffness

K _{vert}	Vertical Stiffness
LT	Lactate Threshold
LTP	Lactate Turnpoint
MVC	Maximal Voluntary Contraction
PERF _{rel}	Performance relative to the winner
PF	Plantar flexors
PFVP	Power-Force-Velocity Profile
P _{max}	Theoretical maximal power derived from the force-velocity profile
P _{met}	Metabolic Power
RCP	Respiratory Compensation Point
RE	Running Economy
RER	Respiratory Exchange Ratio
RPE	Rating of Perceived Exhertion
SF	Step Frequency
UH	Uphill
v_0	Theoretical maximal velocity derived from the force-velocity profile
VA	Voluntary activation
\dot{V}_E	Minute Ventilation
$\dot{V}O_2$	Oxygen Uptake
$\dot{V}O_{2max}$	Maximal Oxygen Uptake
v _{Peak}	Average speed of the last minute of the incremental test
VR	Vertical race
WB	Work of Breathing
WMRA	World Mountain Running Association
z ₁	Zone 1

z_2

Zone 2

z_3

Zone 3

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Préambule

Bien que le trail running et la course sur route soient tous deux des disciplines d'athlétisme dont l'objectif est de couvrir une distance dans le temps le plus court possible et qu'ils soient tous deux des sports régis par World Athletics, il ne s'agit pas réellement du même sport. Le trail running est en général défini comme une course à pied dans un environnement naturel avec un minimum de routes pavées ou asphaltées, ne dépassant pas 20-25% du parcours total de la course. La popularité du trail running a augmenté plus que celle de la course sur route au cours de ces dernières années. Le nombre de participants aux courses de trail running a augmenté au niveau mondial, alors que la croissance de la course sur route a stagné ces dernières années.

Malgré les similitudes apparentes entre la course sur route et le trail, il semble que les athlètes ne remportent pas de courses au plus haut niveau dans ces deux disciplines. Ces différences dans l'identité des vainqueurs des courses de haut niveau pourraient être dues au fait que les récompenses et le prestige sont moindres en trail running. Cependant, il est également possible qu'une partie de la différence entre la course sur route et le trail s'explique par les caractéristiques spécifiques de chaque discipline. La course sur route se pratique normalement sur des routes asphaltées et en milieu urbain, et ont tendance à être plus plates. A l'inverse, la course de trail se pratique principalement en montagne, sur des terrains variés qui peuvent aller de chemins larges à des sentiers étroits et techniques comprenant des obstacles, tels que des rochers ou de la neige.

Au cours de la dernière décennie, l'intérêt pour le trail running a augmenté au sein de la communauté scientifique, et de nombreux articles étudiant les exigences des courses, les déterminants de la performance et les conséquences physiologiques des événements de trail running ont été publiés. L'objectif de cette thèse est d'approfondir les connaissances sur les facteurs de performance de la course à pied prolongée, en se concentrant sur le trail, puis sur les effets de la fatigue induite par la course à pied prolongée sur l'économie de la course.

La première partie de la thèse se concentrera sur les facteurs qui affectent la performance en course de trail. L'introduction (Chapitre 2) vise à donner un aperçu des caractéristiques des épreuves de trail running, en essayant notamment de les comparer aux épreuves de course sur route, qui ont reçu beaucoup plus d'attention dans la littérature. Le Chapitre 3 se concentre sur les déterminants de la performance de la course à pied prolongée, en commençant par une revue de la

littérature sur les exigences d'intensité de la course de trail et les différents facteurs qui influencent la performance, avec une attention particulière sur la course de trail. Des comparaisons de certains déterminants de la performance entre coureurs sur route élite vs coureurs de trail élite (étude 1) et l'étude des facteurs qui influencent la performance dans les courses de trail de différentes distances (étude 2) sont ensuite présentées. Le Chapitre 4 se concentre sur les conséquences de la fatigue induite par la course à pied prolongée, notamment les conséquences sur l'économie de course (RE). En commençant par une revue de la littérature sur les modifications de RE induites par la course à pied prolongée et les mécanismes potentiels conduisant à ces modifications, le chapitre se poursuit en présentant deux autres études réalisées dans le cadre de mon projet de thèse. L'étude 3 montre les conséquences des courses de trail de différentes distances sur RE, tandis que l'étude 4 explore les modifications du coût de la locomotion induites par différentes modalités d'exercice en laboratoire : course à pied vs cyclisme. Enfin, le Chapitre 5 discute des résultats de cette thèse et propose des orientations futures pour la recherche.

1. General introduction

Although trail running and road running are both athletics disciplines with the goal of covering a distance in the shortest time possible and are both governed by World Athletics, they are not the same sport. Trail running is governed by the International Trail Running Association (ITRA), which is recognized by World Athletics as the technical partner in charge of trail running. In addition, trail running is not the only off-road running competitions in the natural environment, since mountain running, skyrunning and fell running also exist. Other federations organize championships in those disciplines, outside the control of the ITRA but still under world athletics, such as the World Mountain Running Association (WMRA), and outside the ITRA and World Athletics, such as the International Skyrunning Federation (ISF) or the Fell Runners Association. However, there is some overlap between the competitions supervised by those federations, and a competition organized under the ISF may still give points in the ITRA rankings. Trail running is defined, in general, as a foot race in a natural environment with minimal paved or asphalt roads, not exceeding 20-25% of the total race course. In the ITRA definition, there are no requirements for race distance or elevation gain. Within this broad definition, other federations include different details in the definitions of their disciplines. For example, the WMRA requires an average incline between 5 and 25%, and distances are restricted to 1-42.2 km, while they allow larger sections on asphalt as long as the incline condition is respected. On the other hand, the ISF requires the races to be in a mountain environment above 2,000 m above sea level, including very technical trails, but if the race has an average incline of $> 6\%$ the race may take place below 2,000 m. The ISF considers three race disciplines, Vertical (uphill races shorter than 5 km), Sky (20-49 km with more than 1300 m of elevation gain) and Ultra (50-99 km with more than 3200 m of elevation gain). More details on the different modalities and federations are included in **Table 1** (Scheer et al., 2020).

Table 1. Summary of characteristics of different off-road running disciplines under different governing bodies. Adapted from Scheer et al. (2020).

Running Discipline	Trail Running	Mountain Running	Fell Running	Skyrunning	Ultramarathon Running
International governing body	ITRA, recognized by WA	WMRA, recognized by WA	Fell Running Association, not recognized by WA	International Skyrunning Federation, not recognized by WA	International Association of Ultrarunners, ITRA, recognized by WA
Race Distance	Any	Up to 42.195 km	< 10 km to any	≤ 99 km	> 42.195 km
Race category	XXS-XXL categories (based on km-efforts)	Classic uphill, classic up & down, vertical, long-distance races	Distance categories L, M, S and orienteering, and ascent categories (A-C)	Sky (20–49 km with 1300 m vertical climb (VC)), Ultra (50–99 km with 3200 VC), Vertical (uphill races of a maximum distance of 5 km)	Single distance, multi-stage, multi-day, timed events
Running Surface	Natural environment with ≤ 20–25 % of paved or asphalted road	Natural environment with ≤ 25 % of paved or asphalted road, exceptions when large elevation change	Road surface ≤ 20– 40 % of total race distance	Mountain environment above 2000 m above sea level	Any- off-road, trail, road, and track
Elevation	Not specified	Average incline should include a minimum of 5 % and not exceed 25 %, with the most preferable average elevation	Not less than 50 m climb/km on average, to not less than 20 m climb/km	Takes place in above 2000 m elevation, with average incline up to 6 % over entire course	N/A
Runners/ year	~13,000,000 [§]	N/A	> 10,000	> 50,000	Approx. 357,000

ITRA, International Trail Running Association; WA, World Athletics; WMRA, World Mountain Running Association; [§]estimated figures worldwide from ITRA.

Trail running has grown in popularity more than road running during the last years. Number of participants and number of races has increased globally (ITRA, n.d.-b) while it has stagnated or started to decrease for road races, increasing from 5 million participants worldwide in 2001, peaking at 9.1 million participants in 2016, and declining to 7.1 million in 2018 (Andersen, 2020). Despite the apparent similarities between road and trail running, it seems that athletes do not win races at the top level in road and trail running. On the contrary, there are several examples of world champions and record holders in the track who have excelled in road running, and a transition from the track to the longer distances on the roads is normal for many athletes (i.e. Haile Gebrselassie, Kenenisa Bekele, Galen Rupp or Eliud Kipchoge). However, it is less common for track and road runners to transition to trail running. Therefore, athletes do not usually succeed in both, trail and road running, but this could be because not the same elite athletes participate. These differences in who the winners are in high-level races could be caused because there is less prize money and prestige in trail running (for example, trail running is not included in the Olympic program, while the Marathon is). This may not attract some of the best runners in the world, as shown by the low participation of east African runners in trail running races. This shows that the general level of performance in the sport may be lower, therefore allowing athletes who would not be able to compete at the highest level in road running to win in trail running.

However, it is also possible that part of the difference between road and trail running is explained by the specific characteristics of each discipline. Compared to road running, trail running is a different sport because of the competition distances, the terrain on which the races happen, the duration and the environment. Road running is normally done on asphalted roads and urban settings, and they tend to be flatter. In contrast, trail running is mainly done in the mountains, over varying terrain that can range from smooth dirt roads and single-track trails to technical trails including obstacles such as rocks or snow.

During the last decade, the interest for trail running has increased among the scientific community, and numerous papers studying the demands of trail running racing, the determinants of trail running performance and the physiological consequences of trail running events have been published. The aim of this thesis is to deepen the knowledge about performance factors of prolonged running, with a focus in trail running, and then a deeper focus on the effects of fatigue induced by prolonged running on running economy (RE).

The first part of the thesis will focus on the factors that affect performance in trail running. The introduction (**Chapter 2**) aims to give an overview of the characteristics of trail running events, especially trying to compare them to road running events, which have received much more attention in the literature. **Chapter 3** focuses on the performance determinants of prolonged running, starting with a review of the literature on the intensity demands of trail running and the different factors that influence performance in prolonged running, with a special focus on trail running. Cross-sectional evidence is then presented on the differences in terms of some of the performance determinants in elite road vs trail runners (Study 1) and the factors that influence performance in trail running races of different distances (Study 2). **Chapter 4** focuses on the consequences of fatigue induced by prolonged running, especially the consequences on RE. Starting with a literature review on the changes in RE induced by prolonged running and the potential mechanisms leading to those changes, the chapter continues presenting two studies performed during my PhD project. Study 3 shows the consequences of trail running races of different distances on RE, while study 4 explores the differences in cost of locomotion induced by different exercise modalities in the laboratory: running vs cycling. Finally, **Chapter 5** discusses the findings of this thesis and proposes future directions for research.

2. Introduction: Characteristics of trail running events

2.1. Course characteristics

The main defining feature of trail running races is that they happen in nature, in trails and mountains, which gives trail running its two main defining factors: the elevation changes along the course and the terrain over which athletes must run. Compared to road races, which are normally run on relatively flat courses, trail running races are commonly run in hilly areas and over mountainous terrain. For example, comparing road to trail races, the elevation gain in the 6 World Marathon Majors ranges 74-269 m over 42.195 km (elevation gain of 1.7 to 6.4 m/km), while the races that formed the Golden Trail series in 2021 had elevation gain ranging 1,700-2,862 m for distances ranging from 21 to 43 km, which is equivalent to an elevation gain of 64.1 to 89.8 m/km, i.e. more than 10 times greater than the steepest of the World Marathon Majors. This greater elevation gain and loss will have an effect of increasing the duration of the events for the same distance, when compared to road races, and likely a change in the mode of contraction and an increase in the role that muscle strength of the lower limbs plays as a determinant of performance, both to propel the body during the uphill sections and to resist muscle damage due to the eccentric contractions during the downhill sections (Vernillo, Giandolini, et al., 2017).

While road races are normally run on asphalt, trail running races are defined by the terrain in which they are run. The organizers of trail running events often design the race courses specifically to minimize the distance run on asphalt, while maximizing the distance run in the natural environment, be it mountain paths, single track, and even sometimes off-trail running. Some sub-disciplines, such as fell-running, are often run off-trail, and skyrunning courses often seek to find sections with snow and very steep inclines, in which ropes or chains are sometimes used for assistance. The runners are thus required to run on different surfaces, including dirt trails, snow, rock slabs, sand, scree and talus; and the trails often include obstacles such as steps, rocks, roots and river crossings that must be navigated, avoided or surpassed (Figure 1).



Figure 1: Examples of terrain and obstacles that are often encountered in trail running races.

This may require trail runners to have better coordination and strength than road runners, and to make technical and tactical decisions to choose the best possible path. It may also be dangerous, since the combination of the terrain and tiredness due to the exertion during the race may lead to worse coordination and decision making, leading to potentially fatal accidents. For example, elite trail runner Hillary Allen fell 50 meters off a ridge during a Skyrace in Norway in 2017, leading to serious injuries which kept her away from the sport for years, and a trail runner did not survive a fall during a technical section of the TDS race at the Ultra Trail du Mont Blanc in 2021. This contrasts with road runners, who compete in a predictable course, with low risk of acute traumatic injuries, and for whom their performance is based on repeating a stride pattern as close to optimal as possible for the duration of the race.

2.2. Environment

In contrast to road racing events, which often happen in urban settings and their surroundings, trail running race courses are often specifically designed to be in nature, often in mountainous terrain. This brings in a set of challenges related to the mountain environment, including altitude, weather and remoteness.

Trail running races are often organized in mountainous regions and at high altitudes, often surpassing 3000 m above sea level at several points during the race. The higher elevations are

associated with hypoxia, due to the lower partial pressure of oxygen (Mazzeo, 2012). Hypoxia is associated with physiological changes including increased heart rate (HR), increased ventilation, increased dehydration, and increased risk of acute mountain sickness (Mazzeo, 2012; Singh et al., 1969), all of which can negatively affect exercise performance.

The mountain weather is another challenge that trail runners must face. Weather in the mountains can be unpredictable and variable, and athletes could face, during the same race, temperatures above 30° C in the valleys and rain, snow, wind, and freezing temperatures in the passes, ridges or summits. Therefore, athletes must carry with them all the necessary equipment to adapt to changing weather. The weather conditions in the mountains have been the cause of numerous tragedies during recent years. In a race in the Spanish Pyrenees in 2012 more than half of the participants had to drop out due to the cold and wet weather, and a female participant died from hypothermia. More recently, in May of 2021, 21 trail runners passed away in a mountain ultramarathon in China, due to a sudden change in weather that included a hailstorm and strong winds. This disaster forced the cancelation of the race and prompted the ban of ultramarathons and mountain and desert trail running races in China. Furthermore, aid stations are often not evenly spaced in trail running races, and athletes can sometimes spend hours between aid stations. Thus, athletes are required to be partially self-sufficient, carrying food and water, as well as the necessary equipment to deal with the environmental conditions.

In contrast, road running races don't usually have great variability in altitude or weather. Therefore, road runners can train specifically to adapt for the likely set of conditions they will encounter on race day, i.e., via altitude or heat acclimation strategies before specific races. Weather conditions are unlikely to be very variable during road running races, therefore runners can often choose their equipment at the beginning of the race, and they do not need to change it during the competition. Furthermore, the availability of aid stations at regular intervals allows road runners to avoid having to carry food or liquids during the race.

2.3. Race Duration and Distance

The most common road race distances range from 5 km to the marathon (42.195 km). World athletics recognizes world records in the distances: 5 km, 10 km, Half Marathon (21.0975 km), Marathon and 100 km. The durations of this events for the best elite road runners range from

under 13 minutes in the 5 km to just above two hours in the marathon, and above 6 hours in the 100 km. Recreational runners often take more than twice as long as the elites to complete the same race distances. In the case of trail running, race distances and durations are much more variable. To start, there is not a set of official distances that count officially for world records. Trail running race courses are often, but not always, designed with a “logical” goal, such as reaching the top of a specific mountain or circumnavigating a mountain massif, not with the goal of reaching an exact distance. Despite that, trail running race distances will often approach a “set” distance, such as approximately 1,000 m of elevation gain or a distance of 40 to 45 km, often called mountain marathons because they approach the marathon distance, and the most popular trail ultramarathon races such as Western States 100, Hardrock 100, La Diagonale des Fous or the Ultra-Trail du Mont-Blanc approach approximately 100 miles (160.9 km). Despite the distances being often similar, the elevation gain and loss and the conditions create longer durations in trail running races, compared to road running. For example, the men’s world record for the vertical kilometer (1,000 m of elevation gain in under 5 km) is 29:42 min. Races in the Golden Trail World Series that approach the marathon distance can have record times much longer than road marathons, for example Zegama-Aizkorri Maratoia (42.185 km, 2736 m+) has a record of 3:45:08 h and the Pikes Peak Marathon (42.180 km, 2382 m+, ascending to 4282 m of elevation) has a record of 3:16:39 h. Furthermore, the distances of the most important races are not set, and can vary from one year to the next. For example, the Trail Running World Championships were contested over a distance of 85 km in 2018 (men’s winning time 8:38:35 h), and 44 km in 2019. Distances beyond the marathon are also more common in trail running, which combined with the terrain lead to much longer race durations being common (Figure 2). The current method to measure the equivalent distance between difference races is used by the ITRA is the km-effort. This method is used to try to account for both, race distance as well as elevation gain, with a single number. According to the ITRA, km-effort for a race are calculated by adding 1 km to the horizontal distance for every 100m of elevation gain, using the formula:

$$\text{Km-effort (km)} = \text{Distance (km)} + (\text{Elevation Gain (m)} / 100)$$

The ITRA states (ITRA, n.d.-a) that the km-effort distance of a race is approximately equivalent to the same race distance on a flat course. Taking the examples mentioned above, Zegama-Aizkorri Maratoia would be equivalent to 69.5 km-effort and Pikes Peak Marathon to 66

km-effort, both races being, in theory, equivalent to distances much longer than a marathon. The longer duration of trail running races will affect the maximum intensity that is sustainable for the duration of the race, as well as the race strategy in terms of nutrition and hydration. The ITRA classifies the races in seven different categories depending on their distance measured in km-effort (Table 2), and these categories are used to establish international performance rankings and points systems.

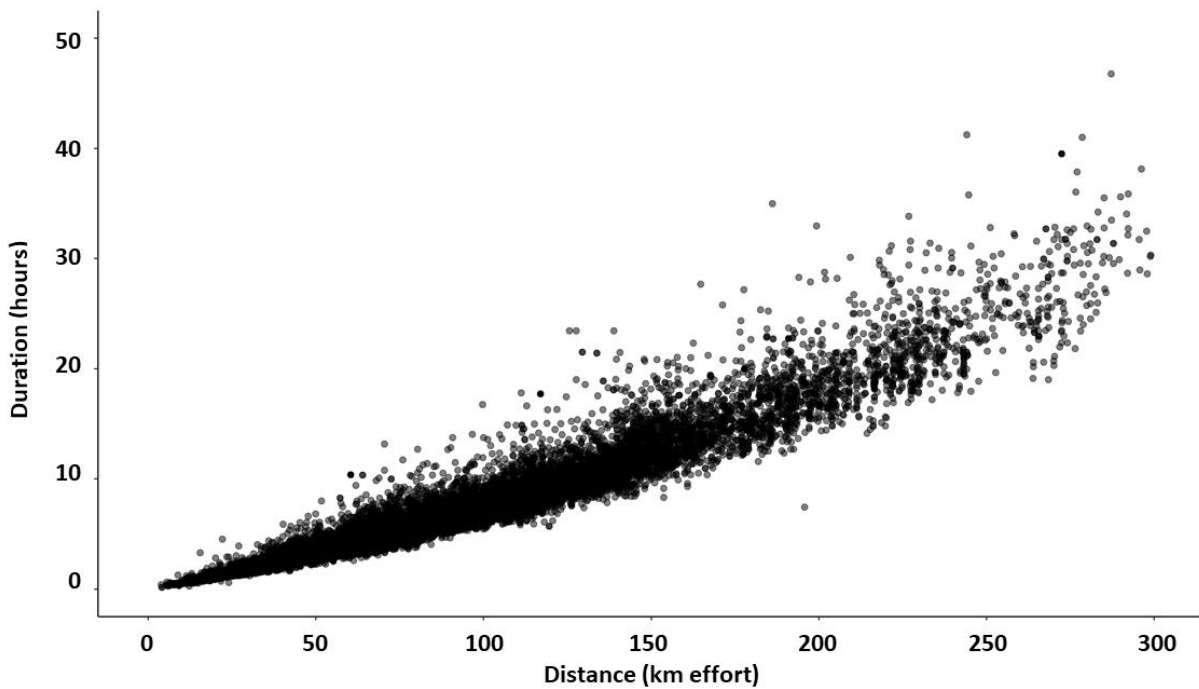


Figure 2. Relationship between race distance (measured in km-effort) and race duration of the winner in all races up to 300 km-effort sanctioned by the ITRA between the years 2010 and 2019.

Table 2. ITRA race category classification.

Approximate Winning Time	Category	Km-effort
1h	XXS	0 – 24
1h30 – 2h30	XS	25 – 44
2h30 – 5h	S	45 – 74
5h – 8h	M	75 – 114
8h – 12h	L	115 – 154
12h – 17h	XL	155 – 209
> 17h	XXL	≥ 210

2.4. Equipment

Due to the peculiarities of the terrain, the mountain environment and the weather conditions trail running requires specific equipment, which is not required during road running races. First, specific trail running shoes are used (Figure 3). They differ from road running shoes by being more protected, often including a plate within the midsole that is stiffer than the surrounding material, designed to protect the bottom of the foot from impacts with sharp rocks and roots. They also often include more protection in the upper of the shoe, including layers that protect the toes from frontal and lateral impacts with objects such as rocks or roots, and sometimes they include a waterproof-breathable membrane. Finally, they have more aggressive outsoles, with deeper lugs, designed for better grip in the mountain terrain. The outsole design is often specific for a type of terrain, with some designs being optimized for dry or rocky terrain, and others for muddy terrain, with even deeper, more spaced lugs. All those specific features can increase the weight of the shoes when comparing them to road-running shoes. However, some brands are already making racing trail-running shoes that are able to rival with road racing flats in terms of weight.



Figure 3. Examples of shoes designed for competition in trail running and road running races. Notice the differences in weight (as reported by the manufacturer), the differences in outsole lug pattern and depth, and the protective overlays in the shoes designed for ultramarathon trail running.

Besides the shoes, trail runners often have to carry extra equipment, although that depends on the event. In shorter races, there is often no extra equipment required. However, some races have a list of mandatory equipment. These lists can vary between races. Some very short races include a minimal list of equipment (i.e. a survival blanket and a windbreaker), while others have extensive lists including extra layers of warm and waterproof clothing, headlamps, mobile phone, a minimum supply of water, whistle, first aid equipment, food and a backpack to carry all the equipment. Beyond this list, some races such as the UTMB® have supplementary lists for hot and cold weather, including extra clothing or more water reserves. All of this equipment that must be carried places specific demands on trail runners. Due to this, runners in longer races must be adapted to racing while carrying a backpack weighing between one and 3-5 kg. The extra weight that is carried will increase the energy requirements of running, since more weight must be displaced, and it may increase the risk of muscle damage during downhill sections, as the muscles are forced to brake greater impact forces.

2.5. Competitive Season

Another potential difference between trail and road running, especially at high levels of performance, is the difference in the frequency of competitions. It seems that top-level road runners, who specialize in the marathon race less often than top-level trail runners. For example, an analysis of the race participation of the world's top-10 marathon runners (best times, extracted from the World Athletics official results website) in 2019 shows that they ran an average of 2.6 ± 1.3 races per year, with a maximum of 5. Out of those, 1.5 ± 0.5 were marathons, with at most two marathons completed in a season. However, looking at the 10 best trail runners according to two different rankings (ITRA ranking and Skyrunning World Series ranking) shows that they ran an average of 7.3 ± 2.5 races, ranging from 4 to 13, with 3.4 ± 1.3 being longer than 40 km. One runner raced only one race > 40 km, while eight of them ran 3 to 5 races > 40 km. Therefore, high-level trail runners seem to compete more frequently, and also to compete more frequently in races longer than 40 km than road runners. This leads to a greater time spent competing every year, which may have implications for training and recovery, and it possibly leads to not peaking for one or two especially important competitions every year, but having to stay in very high form for a longer period. It seems that the schedules of trail runners are more similar to other sports such as triathlon, in which the top-5 men in the professional triathlon union ranking averaged 7.2 ± 1.8 races in 2019, ranging from 5 to 9. Although this raises the question of the physiological consequences of road vs trail running (see below), one possible reason why trail runners may be required to compete more often may be the lower prize money for the winners. For example, the 2006 NYC Marathon had a prize purse totaling more than \$700,000, which included a \$130,000 prize for the winners (World Marathon Majors, 2006). They also include bonuses for running faster than set times and for breaking records and runners often collect appearance fees to compete in the races. Meanwhile, prize money is much less in trail running races. For example, the Ultra Trail du Mont Blanc, arguably the most important trail running race in the world, offers €2000 to the winner in the main race, the UTMB®, and €900 to €1300 to the winners of the other races. Other example prizes from major races include no prize money (Western States Endurance Run, USA), €1000 for the winner (Zegama Aizkorri Mendi Maratoia, Spain), \$15000 for the winner (Run Rabbit Run, USA) and €2000 for the winner of the Skyrunner World Series. This possibly means that trail runners must compete more often than road runners if they want to do it full time, since their main sources of income are probably prize money, which is low, and sponsorship, which requires racing

often to provide exposure for the sponsors. Beyond economic reasons, it is also possible that the nature of trail running races may allow greater competition frequency. For example, the softer terrain compared to the asphalt, or the more variation in the stride and the changes in mode of contraction may contribute to lower impact or muscle damage, allowing for shorter recovery times between races.

Résumé du Chapitre 2

- La course sur route et la course de trail sont des sports différents dont les caractéristiques peuvent nécessiter un entraînement et des adaptations spécifiques.
- La course de trail implique des dénivellations beaucoup plus importantes que la course sur route. En outre, les courses de trail comprennent une variété de terrains et d'obstacles, notamment du sable, des rochers, des arbres, des racines, de la neige et des traversées de rivière.
- Les courses de trail se déroulent souvent en montagne, ce qui entraîne des défis environnementaux, notamment l'hypoxie associée à l'altitude, ainsi que le climat de montagne, qui peut provoquer des changements de température et des précipitations, entraînant des pertes de performance et des accidents.
- La durée et la distance des courses sont beaucoup plus variables et souvent plus longues en trail running qu'en course sur route. Les championnats du monde de trail running se déroulent souvent sur des distances allant de 40 à 90 km, et certaines des courses les plus prestigieuses approchent ou dépassent les 100 miles.
- Les coureurs de trail utilisent un équipement spécialisé pendant les courses, pour transporter de la nourriture et avoir une meilleure adaptation aux conditions environnementales. Cela oblige les coureurs de trail à porter des poids plus lourds pendant les courses que les coureurs sur route.
- Les meilleurs coureurs de trail participent généralement à plus de compétitions annuellement que les meilleurs coureurs sur route. Cela peut être dû à des raisons économiques, ou à des besoins de récupération réduits en raison de la variété du terrain.

3. Physiology of Trail and Road running performance

3.1.Race intensity in Road and Trail Running

It is well known that there is a relationship between the duration of exercise and the highest intensity that can be sustained for that given duration (Burnley & Jones, 2016; Hill, 1925; Hill, 1993). This relationship is termed the intensity-duration relationship and, for relatively short durations between approximately 2 and 30 minutes, it is well described by the critical power or critical speed model (Burnley & Jones, 2016; Galbraith et al., 2014; D. Hill, 1993). Several studies have measured intensity during running races over short distances on the road or track, or laboratory tests on level treadmills, using different methods. Furthermore, different methods to report intensity have been used. Some studies report speed relative to maximal aerobic speed or $\dot{V}O_2\text{max}$, while others report speed relative to critical speed (the speed equivalent to the asymptote of the hyperbolic curve describing the speed-duration relationship in running, Jones & Vanhatalo, 2017), and others report average HR during the event, relative to maximum HR, which sometimes makes it difficult to make comparisons between studies. Furthermore, other studies have reported the estimated time or percentage of total duration spent in a given intensity domain. To do this, the intensity spectrum is divided in three training zones, corresponding to the exercise intensity domains (Seiler & Kjerland, 2006). Zone 1 (z1) corresponds to the moderate intensity domain, below the gas exchange threshold or lactate threshold; zone 2 (z2) corresponds to the heavy intensity domain, between the GET and the second threshold (respiratory compensation point, maximum lactate steady state, lactate turnpoint, critical power, depending on the method of measurement); zone 3 (z3) corresponds to the severe intensity domain, above the second threshold. The boundaries between zones are usually assessed via physiological testing and then anchored to a reference point that can be tracked during exercise, for example a value of HR, power output or speed, with HR being the most commonly used variable when evaluating intensity in trail running races. This is probably due to the fact that speed during trail running is strongly affected by the hilly terrain, and a runner can be in a different intensity domain in two situations in which they are running at the same speed. A similar approach, setting zones based on HR, is often used in other sports in which speed and power are not reliable indicators of physiology, such as cross country skiing (Sylta et al., 2014) and rowing (Plews et al., 2014).

3.1.1. Intensity during road running races

Lacour et al. (1990) found, in a group of elite middle-distance runners (within 10% of the best French performance during the previous season), that the average speed sustained during races was equivalent to $119.1 \pm 5.9\%$ of the maximum aerobic speed during 800 m races, $108.9 \pm 3.5\%$ during 1500 m, $100.5 \pm 3.5\%$ during 3000 m and $97.7 \pm 2.6\%$ in 5000 m (Figure 4). Other studies have measured the relative intensity during short-distance endurance running. For example, Stoa et al. (Støa et al., 2010) found that running speed in a 5 km race elicited $97.3 \pm 2.6\%$ of $\dot{V}O_2\text{max}$ in elite runners with an average performance of 15:06 min, and Davies and Thompson (Davies & Thompson, 1979) found that 5 km speed corresponded to $93.6 \pm 3.2\%$ of $\dot{V}O_2\text{max}$ in 13 male athletes with an average time of 15:50 min.

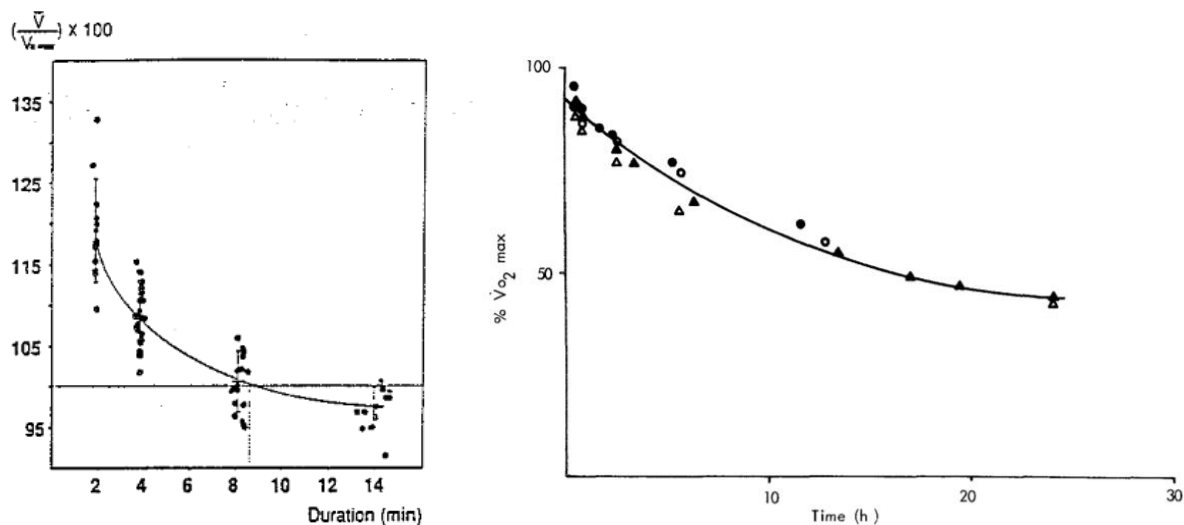


Figure 4. Relationship between running time and speed expressed as percentage of maximum aerobic speed in elite middle-distance runners in races ranging from 800 to 5000 m (left) and relationship of sustainable aerobic power output ($\% \dot{V}O_2\text{max}$) in relation to time in four elite ultralong-distance athletes (right). From Lacour et al., (1990) and Davies and Thompson (1979).

In the marathon distance, Jones and Vanhatalo (2017) suggested that elite marathon runners are able to sustain an intensity equivalent to about 96% of their critical speed, meaning that they complete the marathon in the heavy intensity domain, i.e. z2. Davies and Thompson (1979) reported a speed equivalent to $81.9 \pm 3.2\%$ of $\dot{V}O_2\text{max}$ in male marathon runners averaging $\sim 2:30$ h for the marathon, and $78.7 \pm 6.6\%$ of $\dot{V}O_2\text{max}$ in females averaging $\sim 3:09$ h. Smyth and Muniz Pumares (2020) analysed training and racing data from more than 25,000 runners and found that

faster runners raced the marathon closer to critical speed than slower runners. Runners who finished in 2:30 h ran at 93.0% of critical speed, while runners who finished in 6 h ran at 78.9% of critical speed (Figure 5).

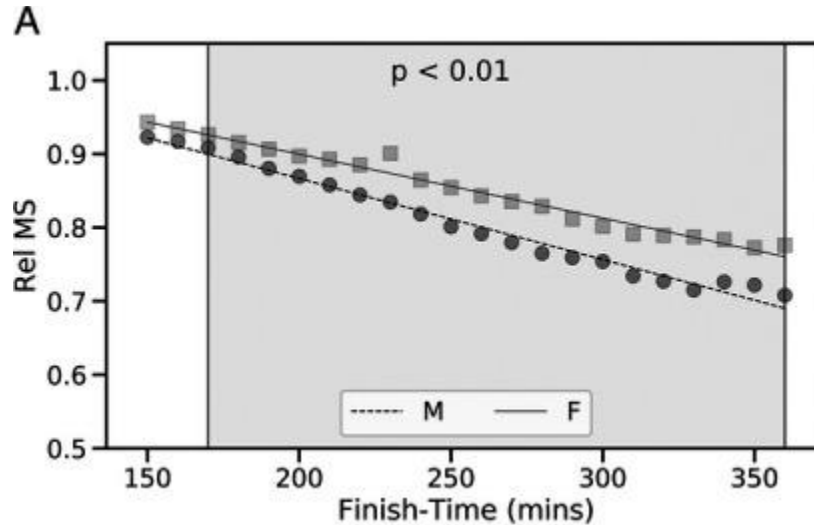


Figure 5. Relative marathon speed (Rel MS) of male (M) and female (F) runners for different marathon durations. Rel MS is expressed as marathon speed divided by critical speed. Adapted from Smyth and Muniz-Pumares (2020).

In distances beyond the marathon, Davies and Thompson (1979) reported an average speed equivalent to $67.1 \pm 5.8\%$ of $\dot{V}O_2\text{max}$ during an 84.4 km race completed in $\sim 5:58$ h, on average, by the same 13 runners mentioned previously. Sengoku et al. (2015) studied two subjects in a 100 km road race. The runners finished in approximately 7 and 9 hours, and they averaged speeds equivalent to 89.9 and 78.4% of the lactate threshold, respectively. Millet et al. (2011) found that during 24 h of treadmill runner subjects ran at an average speed equivalent to $39 \pm 4\%$ of the speed associated with $\dot{V}O_2\text{max}$ when considering only the effective running time, and the average speed was $34 \pm 2\%$ when considering the 24 h.

Although different studies using different units to measure intensity makes it difficult to compare between studies, the same general trend emerges. The data from the different road running experiments shows that the maximal sustainable intensity depends on the duration of the race, with longer durations requiring lower intensities. Observing data from the world records and best performances in the distances recognized by World Athletics and the International Association of Ultrarunners confirms the results obtained by the research, showing a continuous drop in speed

with increasing distance (Figure 6). Therefore, considering that the duration of trail running races tends to be longer than that of road races due to longer distances and greater elevation changes, the overall intensity should be expected to be lower during trail running races.

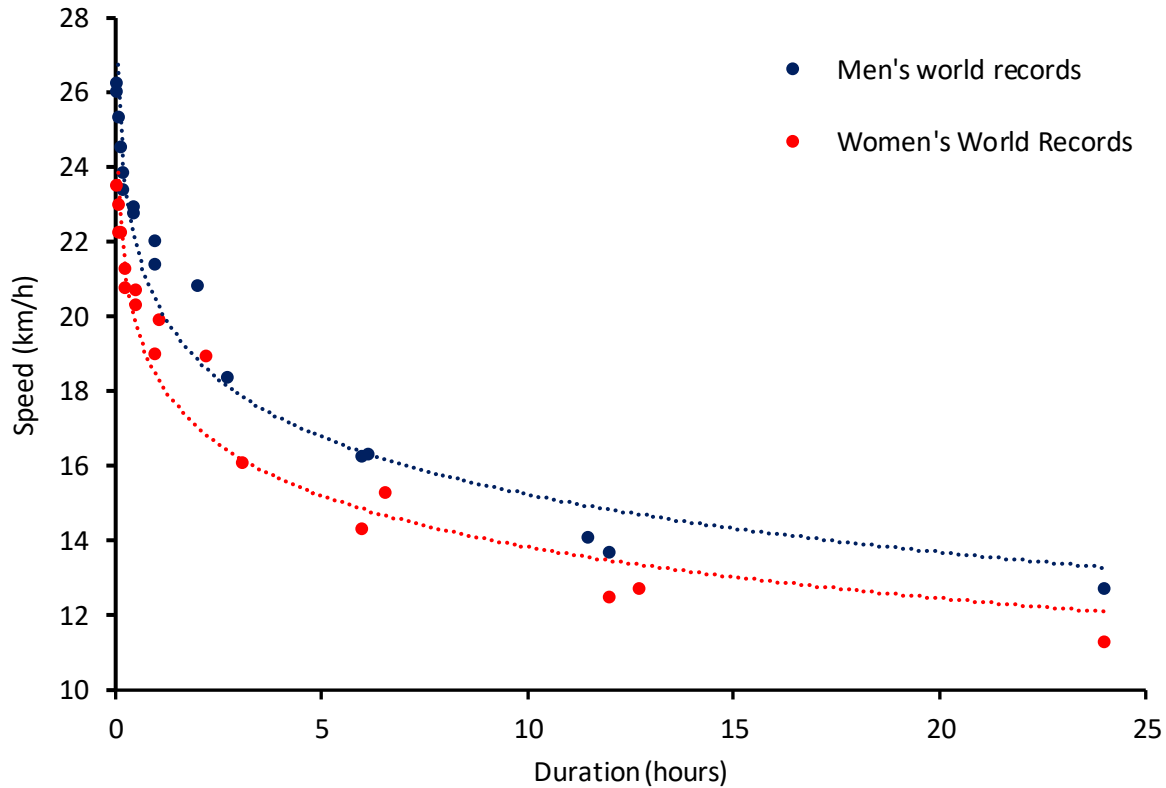


Figure 6. Relationship between performance speed and race duration for World Record and World Best performances in races ranging from 1500m to 24 h for men and women.

3.1.2. Intensity during trail running races.

A few studies have measured the intensity of competition during trail running races. The most important determinants of the intensity during trail running races seem to be duration/distance. Ehrstrom et al. (Ehrström et al., 2018) found that the average HR was 89.8% of HRmax during a 27 km race with 1400 m of elevation, but they did not measure time in each zone.

Rodríguez Marroyo et al. (2018) measured exercise intensity using HR monitoring during the races of a whole season in 7 experienced runners, measuring races that they divided in 4 different categories: vertical races (VR, uphill only races of ~5 km and 1000 m of elevation gain), 10-25 km, 25-45 km and > 45 km races. They found (Figure 7) that the percentage of time spent

in z1 increased as the races got longer, while the percentage of time spent in z2 was greater in races > 45 km. Percentage of time spent in z3 was highest in VR and decreased as races got longer. Interestingly, the total time in z3 was not different between races, and it approached 50 min independently of race distance. There were no differences in the peak HR achieved between races, while average HR, expressed as percentage of HRmax, was 92% for VR, 89.5% for 10-25 km, 84% for 25-45 km, 79% for > 45.

Ramos-Campo et al. (2016) described the intensity distribution of a 54 km trail running race with 2,726 m of elevation gain, which was completed in 6:44 ± 0:28 h. The zones were not divided according to previously measured thresholds, but using arbitrary percentages of HR reserve (HRR), demarcating 4 HR zones (< 50%, 50-70%, 70-90%, > 90%). The average HR during the race was 82% of HRmax. Relative time in zones was 8.5% < 50%r HRR, 25.5% between 50-70% HRR, 51% 70-90% HRR, and 12.5% > 90% HRR. In Figure 7, the four zones described in this study have been simplified into 3 zones, considering that z1 was < 70% HRR and z3 was equivalent to > 90% HRR, since this zone division is what the authors were trying to approximate. Another study by Fornasiero et al. (2018) measured the HR of 12 trail runners (8 males) during a 65 km trail running race with 4000 m of elevation. The average HR during the race was 77% of HRmax, and they spent most of their time in z1 (85.7%) and a negligible amount of time in z3 (0.4%).

The longest race distance for which intensity has been reported is 120 km with 7,554 m of elevation gain. Gatterer et al. (2020) reported intensity for two races that were completed in the same area and at the same time, the abovementioned 120 km race (N = 4) and a 67 km race (N = 11) with 4,260 m of elevation gain. Intensity zones were created relative to the ventilatory thresholds and they found that most of the time was spent in z1 in the 120 km race, while in the 67 km race most of the time was spent in z2 (Figure 7). Average HR during the races was not reported in this study. At least one other study has reported only average HR during trail running races, without an analysis of time spent in each zone.

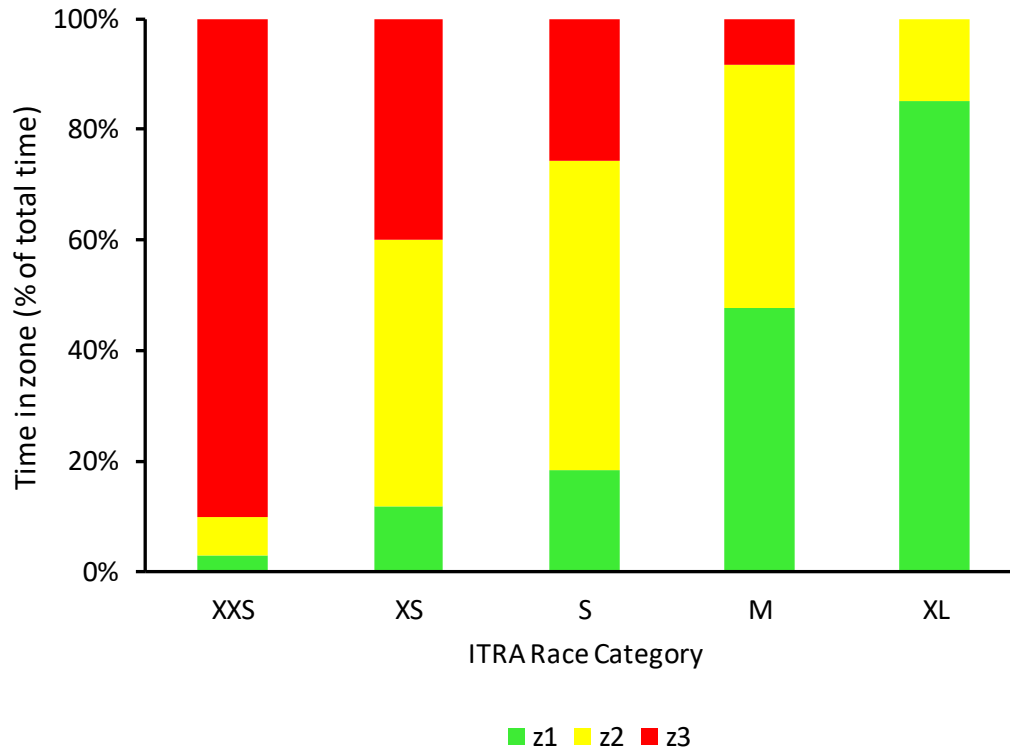


Figure 7. Time spent in zone during trail running races of different ITRA categories. The data from the published studies that reported time in zone has been summarized, classifying the races according to their ITRA race category.

The research to date shows that time spent in z3 tends to decrease as the duration and distance of the competitions increase. However, as Rodriguez-Marroyo et al. (2018) reported, it may be possible to spend a total of around ~50 minutes in z3, in competitions up to 110 km-effort. They suggested this may indicate the existence of an upper limit to the time that can be spent at thigh-intensity when trying to optimize performance in trail runners, implying that runners may have a maximum of about 50 min of time that they can spend in z3 in a race, and those 50 min can be distributed differently depending on the length of the race. They cited Ramos-Campos et al. (2016) to note that the time in z3 in their study also approximated 50 minutes. Pooling the data from the different studies that have reported intensity as percentage of HRmax during trail running races it seems that intensity is negatively correlated to race distance, measured as km-effort, and that the percentage of time spent in z3 decreases abruptly as distance increases (Figure 8). From the results of the best elite athletes in the world, it is also observed that a relationship similar to that found in road running is evident. The performance speed of the best performers in trail running

paces decreases in a similar fashion as that of the best road runners with increasing duration. Figure 9 shows the speed, measured in km-effort/h, of the male winners of trail running races of different durations. To make it comparable to road-running records, only the best athletes are included, with ITRA performance indices greater than 900¹. A similar decline in speed as duration increases is seen in elite trail runners compared to world-record track and road runners (Figure 6).

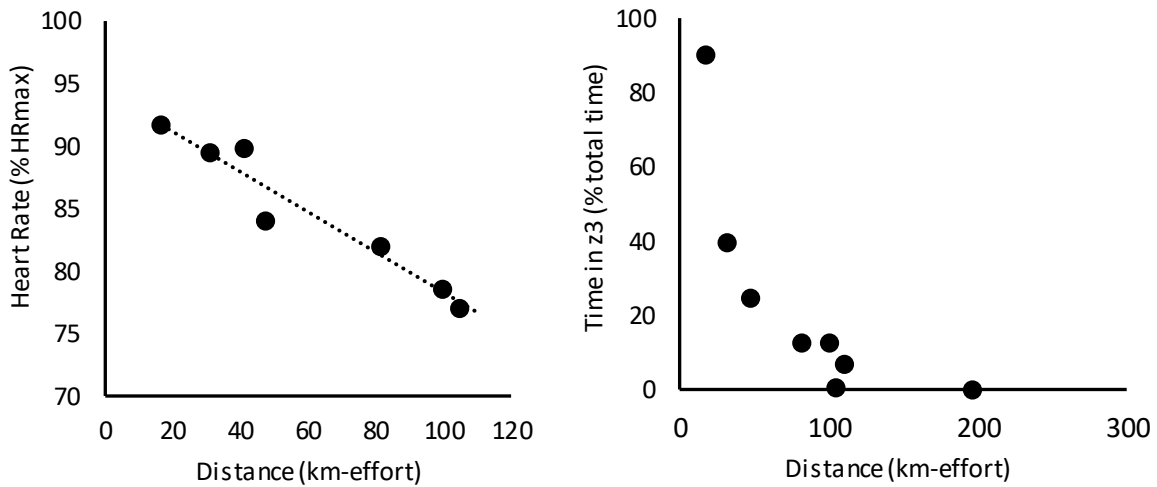


Figure 8. Relationship between percentage of maximal heart rate (HRmax) during the race and race distance measured in km-effort in published research reporting average intensity during trail running races (left) and relationship between time spent in z3 and race distance measured in km-effort in studies which reported time in zone during trail running races (right).

¹Only the best 33 athletes worldwide had a performance index above 900 in 2019.

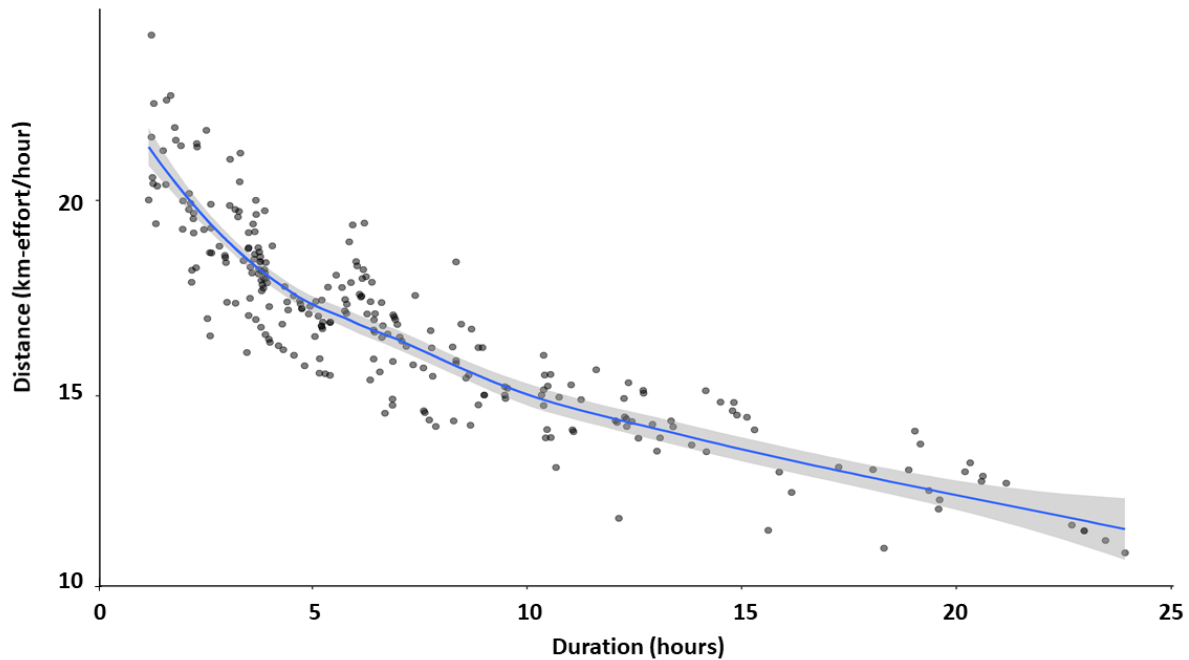


Figure 9. Relationship between speed of the winner, measured in km-effort/hour, and race duration of elite runners (ITRA performance index > 900) in races sanctioned by the ITRA between 2013 and 2019.

Finally, an interesting aspect of competition intensity in trail running is the variation of intensity during races. The research to date does not specify how intensity varies over the race, that is, how athletes pace their efforts. It is not known if intensity is different during uphill, downhill, or flat sections, or if races tend to be paced evenly, or faster at the start or the end. For example, intensity during downhill sections may be limited in some sections by technical terrain and obstacles preventing the athletes from achieving high speeds. This limitation could allow trail runners to recover from a cardio-respiratory perspective, due to the lower intensity, leading to increased effort during uphill sections of races. An example of this is shown in Figure 10 and Figure 11, which represent data collected from trail runners during a mountain marathon (Figure 10) and a mountain ultramarathon (Figure 11). Figure 10 shows that as altitude increases during the uphill section at the beginning of the race, until approximately 1 h 40 min and 16 km, HR remains elevated. After this section, the race continues downhill for the next ~5 km and, while speed remains high, HR decreases. This pattern is then repeated, with higher intensity during the

uphill sections and lower intensity during the downhill section at kilometer 28. Interestingly, this runner spent 47:01 min in z3 during this race, approaching the 50 min suggested by Rodríguez-Marroyo et al. (2018). Figure 11 shows a rapid increase in HR at the start of the race and a progressive decline of HR throughout the race, possibly reflecting the need to slow down the pace as the race progresses. Furthermore, a similar pattern of HR response to uphill and downhill sections is observed, with HR increasing during uphill sections and decreasing during downhills.

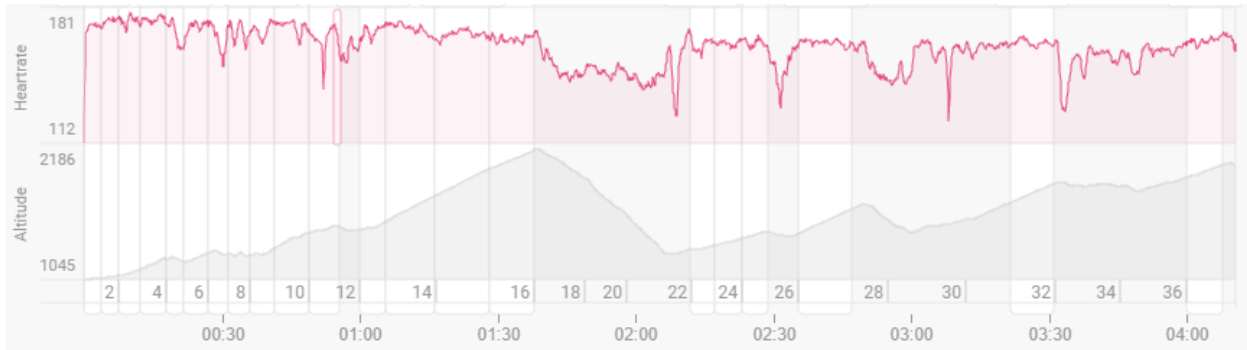


Figure 10. Example of data from a trail runner during the Marathon du Mont Blanc trail running race. Data includes, from top to bottom: heart rate (bpm), and altitude (m). A decrease in HR during downhill sections can be observed after the black vertical lines, showing a decrease in cardiovascular intensity.

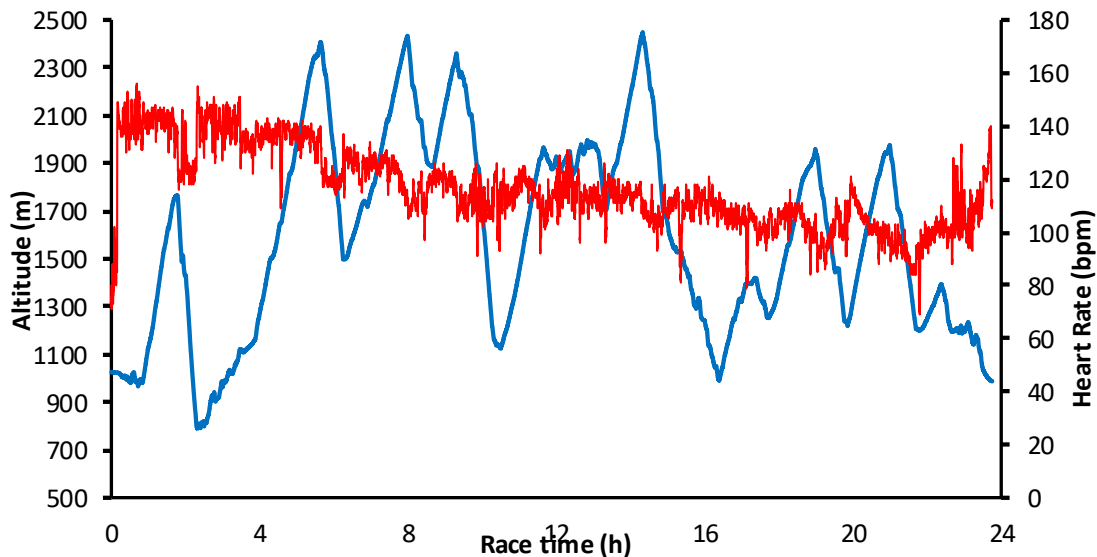


Figure 11. Example of altitude (blue) and heart rate (red) data from a trail runner during the Ultra Trail du Mont Blanc. Two HR trends can be observed: (i) a decrease in HR during downhill sections compared to uphill sections and (ii) a decrease in HR throughout the race.

3.2. Physiological determinants of trail running performance

Most of the energy used in road and trail running events is provided by the aerobic metabolism, since it is the most important energy source in all running events longer than about 60 s (Duffield et al., 2005b, 2005a). The highest performance velocity that can be sustained in long-distance running events is mainly determined by the interaction of three main factors: $\dot{V}O_2\text{max}$, fractional utilization of $\dot{V}O_2\text{max}$ and RE (Bassett & Howley, 2000; Jones & Carter, 2000; Joyner & Coyle, 2008) (Figure 12). The combination of these three variables has been shown to explain 95.4% and 94.9% of the variance in performance in a 16 km time-trial (McLaughlin et al., 2010) and a half marathon race (Gómez-Molina et al., 2017), respectively. The relative importance of each of the determinants of performance seems to depend on the duration of the event. Davies and Thompson (1979) studied the relative importance of each variable in races ranging from 5 km to 84.64 km and found that $\dot{V}O_2\text{max}$ was the most important predictor in 5 km races, and its importance decreased as race distance increased, while the importance of RE increased with longer distances. Furthermore, Pollock et al. (1977) found that marathon runners had better RE, but lower $\dot{V}O_2\text{max}$, than track runners. This trend may change for races of very long distance, since Millet et al. (2011) found that $\dot{V}O_2\text{max}$ was a significant predictor of performance in a 24 h treadmill running test, while there was no relationship between performance and RE. Furthermore, it has been suggested that performance in ultramarathon races, including trail and mountain ultramarathons, is possibly more complex and includes several other factors that are not considered in the simplified physiological model. Most importantly, those include susceptibility to gastrointestinal disorders, muscle and osteoarticular damage and psychological and motivational factors (Figure 13, (Millet, 2011)).

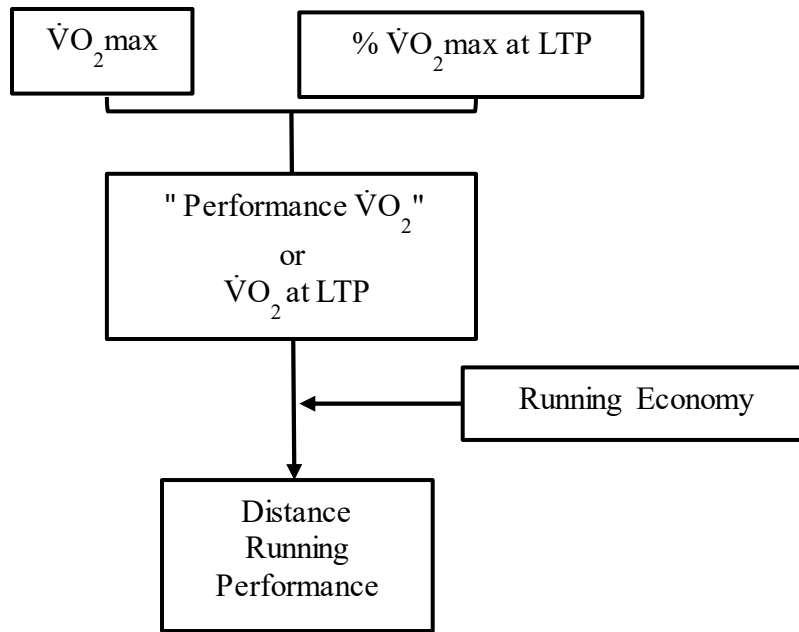


Figure 12. Simplified diagram of the relationship between physiological predictors and performance in distance running. Adapted from Basset and Howley (2000).

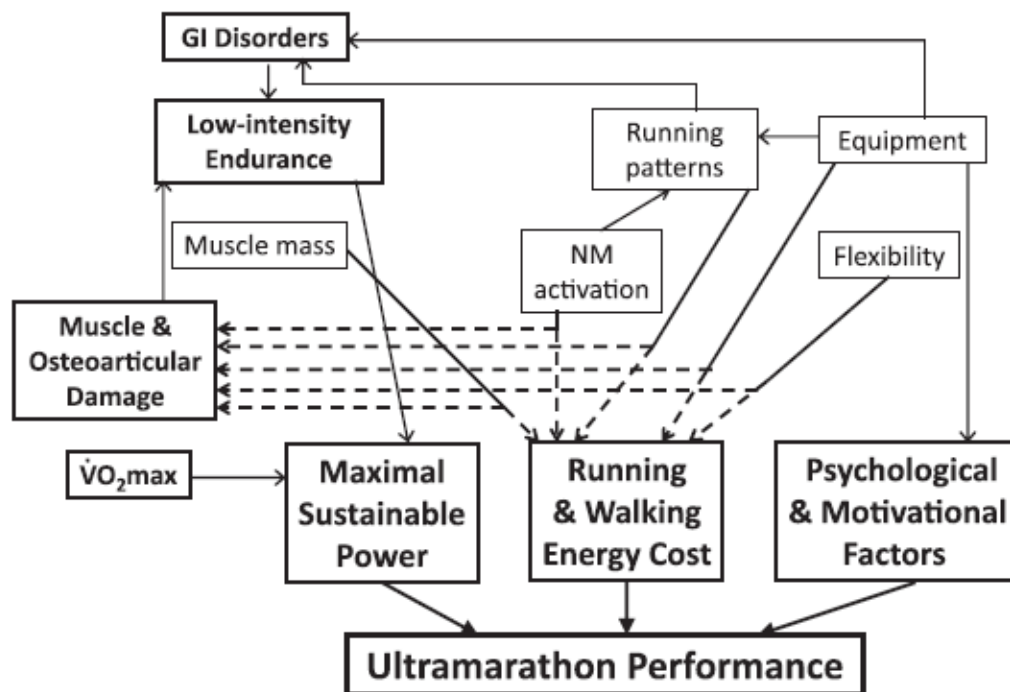


Figure 13. Determinants of performance in ultramarathons. The dashed lines represent factors that may influence a compromise between improving exercise economy and reducing muscle and osteoarticular damage. From Millet (2011).

3.2.1. Maximal Oxygen Uptake

Maximal oxygen uptake is the highest rate at which oxygen can be used by the body during whole body exercise to synthesize ATP through oxidation in the mitochondria (Bassett & Howley, 2000). It has been known for a long time that $\dot{V}O_{2\max}$ is greater in high-level endurance athletes, with values ranging from 70 to 85 ml/kg/min often reported for elite runners (Joyner & Coyle, 2008; Pollock, 1977). Values in the general population tend to be lower, approaching 60 ml/kg/min for trained recreational endurance athletes and about 40 ml/kg/min for untrained young men (Loe et al., 2013). Therefore, $\dot{V}O_{2\max}$ has been identified as a good performance predictor in heterogeneous populations (Foster et al., 1978) and a high $\dot{V}O_{2\max}$ seems to be necessary for elite endurance performance (Jones, 2006; Joyner & Coyle, 2008). The assessment of $\dot{V}O_{2\max}$ often includes an incremental exercise test in which the intensity is increased at regular intervals until exhaustion, while gas exchanges are measured using a metabolic cart.

$\dot{V}O_{2\max}$ is determined by the delivery of oxygen to the active muscles and the extraction and utilization of oxygen by the muscles (Figure 14, (Bassett & Howley, 2000)). The main factors that limit $\dot{V}O_{2\max}$ are central and related to oxygen delivery, including pulmonary diffusion capacity (in elite athletes or when running at altitude), cardiac output (Andersen & Saltin, 1985; Blomqvist & Saltin, 1983), O_2 carrying capacity, which is mainly influenced by hemoglobin mass (Schmidt & Prommer, 2008), and capillary density (Andersen & Henriksson, 1977), which all limit oxygen delivery; while factors related to oxygen extraction and utilization, such as mitochondrial content and the activity of oxidative enzymes in the skeletal muscles seem to be of less importance in trained individuals (Saltin, 1985).

Maximal oxygen uptake in trail running

Maximal oxygen uptake is the variable that has been shown to be associated with trail running performance most consistently. De Waal et al. (2021) reviewed the literature on physiological indicators of trail running performance. They found that in 5 out of 7 studies reviewed, including distances ranging from 7 to 65 km, there was an association of trail running performance with $\dot{V}O_{2\max}$ (Alvero-Cruz et al., 2019; Björklund et al., 2019; Ehrström et al., 2018; Fornasiero et al., 2018; Scheer, Janssen, et al., 2019). Another 4 studies that were not included in the review also showed correlations between $\dot{V}O_{2\max}$ and race performance in distances of 7, 50, 67, 80 and 107 km (Coates et al., 2021; Gatterer et al., 2020; Lazzer et al., 2012; Martinez-Navarro

et al., 2020). Furthermore, in 5 of those studies, $\dot{V}O_{2\max}$ was included in the performance prediction models (Alvero-Cruz et al., 2019; Ehrström et al., 2018; Fornasiero et al., 2018; Lazzar et al., 2012; Martinez-Navarro et al., 2020; Scheer, Janssen, et al., 2019). However, one group of 7 runners in the study by Gatterer et al. (2020) completed a 121 km race, in an average time of 27:49 h, and no correlation between $\dot{V}O_{2\max}$ and performance was found (2020).

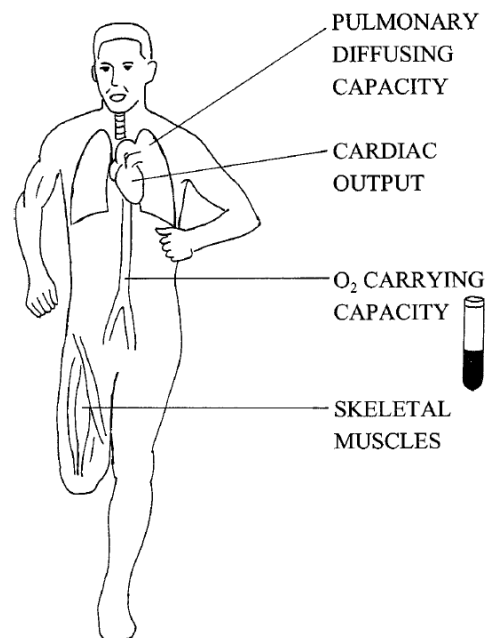


Figure 14. Physiological factors that potentially limit maximum oxygen uptake during whole body exercise in humans. From Basset and Howley (2000).

A few of the previously mentioned studies also evaluated velocity or power at $\dot{V}O_{2\max}$, while one more study did not directly assess $\dot{V}O_{2\max}$, but maximal aerobic speed through a field test (Balducci, Cléménçon, et al., 2017). All of those studies found a high correlation between a measure of maximal aerobic speed or power derived from an incremental running test and $\dot{V}O_{2\max}$ (Alvero-Cruz et al., 2019; Balducci, Cléménçon, et al., 2017; Björklund et al., 2019; Coates et al., 2021; Ehrström et al., 2018; Martinez-Navarro et al., 2020; Scheer, Janssen, et al., 2019). Velocity or power associated with $\dot{V}O_{2\max}$ was a performance predictor in 3 studies, in races of 27, 31, 50 and 80 km (Alvero-Cruz et al., 2019; Coates et al., 2021; Scheer, Janssen, et al., 2019). Coates et al. (2021) also had 8 runners perform a 160 km race and, contrary to the 50 and 80 km races, there

was no relationship between performance and velocity at $\dot{V}O_{2\max}$ in that race distance. These data seem to show that $\dot{V}O_{2\max}$ is a significant predictor of performance in trail running races, at least up to approximately 110 km. However, it is important to consider that in all these studies $\dot{V}O_{2\max}$ was assessed in heterogeneous groups of runners, in terms of performance levels or $\dot{V}O_{2\max}$ values. Therefore, there is still no evidence that $\dot{V}O_{2\max}$ is still a good predictor of performance in more homogeneous groups, such as elite-level trail runners.

3.2.2. Fractional utilization of $\dot{V}O_{2\max}$, lactate and ventilatory thresholds.

Fractional utilization is defined as the percentage of $\dot{V}O_{2\max}$ that can be sustained during a race, and it has been shown to be a predictor of performance in running events (Maughan & Leiper, 1983; Millet et al., 2011). However, other studies have shown no relationship between fractional utilization at race speed and race performance (Støa et al., 2010). Fractional utilization has been associated with different markers of metabolic thresholds, including markers of blood lactate accumulation and ventilatory thresholds (Jones & Carter, 2000).

As exercise intensity increases during an incremental test, there is an increase in anaerobic glycolysis, and therefore an increase in lactate production. To compensate for the increase in lactate production, there is an increase in lactate uptake to be used as fuel by other muscle fibers, the heart and the brain, as well as by the liver for gluconeogenesis (Poole et al., 2020). At lower intensities the rate of clearance matches the increase in lactate production, so the lactate levels in the blood remain stable and close to resting values (1 mmol/l). As intensity increases, the rate of lactate production increases more than that of clearance, and there is an increase above the baseline value, defined as the lactate threshold (LT). Further increases in intensity above the LT will lead to an increased lactate concentration above baseline, but it will remain stable if exercise intensity is maintained over time, achieving a balance between lactate production and clearance. If intensity keeps increasing there will be a second breakpoint in blood lactate concentration which represents the second metabolic threshold, or lactate turnpoint (LTP) (Poole et al., 2020; Svedahl & MacIntosh, 2003). Exercise above this intensity leads to continuous accumulation of lactate until exhaustion occurs. Other methods using lactate have been used to measure the second metabolic threshold, leading to different names for the same concept, such as the maximal lactate steady state (Beneke, 2003; Keir et al., 2015; Svedahl & MacIntosh, 2003) and the onset of blood lactate accumulation (Heck et al., 1985; Sjodin & Jacobs, 1981).

Other methods, using gas exchange measurements, are used to identify the metabolic thresholds during incremental exercise. Those are based on the ideas that above the metabolic thresholds the changes at the level of the muscle or the blood are reflected at mouth level and can be identified by the measurement of expired gasses. As lactate starts accumulating, there is an increase in hydrogen ions (H^+) i.e. a decrease in pH (Robergs et al., 2004), which may contribute to muscle fatigue, together with the accumulation of inorganic phosphate (Westerblad et al., 2002). These H^+ are buffered in the blood using bicarbonate (HCO_3^-), producing water and CO_2 as end-products. CO_2 is then eliminated through breathing (Wasserman et al., 1973). The need for elimination of CO_2 leads to increases in the CO_2 expired to O_2 used ratio, disproportionate increases in ventilation for the increase in workload, changes in the ratios of $\dot{V}_E/\dot{V}O_2$ and $\dot{V}_E/\dot{V}CO_2$, as well as changes in the end tidal partial pressures of O_2 and CO_2 (Binder et al., 2008; Wasserman et al., 1994). These changes in ventilatory parameters can be used to identify the metabolic thresholds, and two thresholds can be identified. The gas exchange threshold (GET) corresponds to the first increase in the slope of \dot{V}_E relative to workload, the increase in the slope of $\dot{V}CO_2/\dot{V}O_2$, the increase of $\dot{V}_E/\dot{V}O_2$, as well as the increase of end tidal partial pressure of O_2 , and it correlates well with the LT. The respiratory compensation point (RCP) corresponds to the LTP and is indicated by a second disproportionate increase in \dot{V}_E /workload, an increase in $\dot{V}_E/\dot{V}CO_2$, and a decrease in end tidal partial pressure of CO_2 , although the cause and effect relationship between lactate accumulation and ventilatory changes with increased intensity is not clear (Neary et al., 1985).

The intensity relative to $\dot{V}O_{2max}$ at which the thresholds occur varies between individuals (Iannetta, Inglis, et al., 2019). It has been reported that LT can be as high as 80-85% of $\dot{V}O_{2max}$ in elite runners (Ingham et al., 2008; Jones et al., 2021; Sjodin & Svedenhag, 1985). Endurance training can decrease lactate production and increase clearance at a given relative intensity, therefore increasing the relative intensity at which the thresholds occur (Hurley et al., 1984). The improvements in the thresholds of trained people seem to be mostly related to changes at the muscle level such as improved oxidative capacity of the mitochondria and improved lactate transportation (Hawley, 2002). The relationship between thresholds, measured using different methods, and performance was reviewed by Faude et al. (2009). They found a strong relationship between either lactate threshold velocity or $\dot{V}O_2$ and running performance, in distances ranging from 800 m to the marathon, with a tendency for higher correlations in long-distance competitions

(half marathon and marathon, range of $r = 0.68$ to 0.98) than in middle-distance races (800-3200 m, range of $r = 0.43$ - 0.93).

Thresholds and fractional utilization in trail running

Four of the studies reviewed by de Waal et al. (2021) found a relationship between metabolic thresholds and trail running performance (Ehrström et al., 2018; Fornasiero et al., 2018; Scheer, Janssen, et al., 2019; Scheer, Vieluf, et al., 2019) in distances between 21 and 65 km. Other studies that were not included in the review by de Waal et al. have also found a correlation between performance and velocity at RCP in a 107 km race (Martinez-Navarro et al., 2020) and $\dot{V}O_2$ at RCP in a 68 km race (Gatterer et al., 2020). Two studies did not assess metabolic thresholds, but found a relationship between higher fractional utilization and performance over 75 km (Balducci, Cléménçon, et al., 2017) and a 3-day stage race covering a total of 90 km (Lizzer et al., 2012).

3.2.3. Running economy

Running economy is a measure of how much of the energy consumed by the exercising athlete is converted into work and used for displacement during running. In other words, it is a measure of how much energy it costs to perform a given running task, such as running one kilometer. It can be measured in several ways, including the $\dot{V}O_2$ required to sustain a given intensity, the oxygen cost of covering a given distance (O_2C) or the energy cost of covering a given distance (Cr). RE is an important determinant of endurance running performance (Bassett & Howley, 2000; Conley & Krahenbul, 1980; Ingham et al., 2008; Jones, 2006; Jones & Carter, 2000; Joyner & Coyle, 2008), accounting for up to 65% of the variance in performance over 10 km in a homogenous population of highly trained runners (Conley & Krahenbul, 1980) and combining $\dot{V}O_{2max}$ and RE accounted for 96% of the variance in performance in high-level middle-distance runners (Ingham et al., 2008).

While RE tends to be better in higher level and elite runners than in lower level runners or untrained runners (Morgan et al., 1995; Pollock, 1977), there is a high variation between individuals (Morgan et al., 1995). Very low values of 150 and 165 ml/kg/km, quantified as oxygen cost, have been measured in world record holders in the half marathon and the marathon (Jones, 2006; Lucia et al., 2008), suggesting that RE is a key factor in top-level performance in road running. An O_2C of 200 ml/kg/min is considered to be average for runners, and values above and

below 200 are considered bad and good economy, respectively (Jones, 2006). Values of 180-195 ml/kg/km are commonly observed in elite runners, reflecting their good RE (Jones et al., 2021; Morgan et al., 1995; Pollock, 1977; Tam et al., 2012). RE seems to be the most predictive variable of running performance within groups of well-trained athletes, which all have similarly high $\dot{V}O_2\text{max}$ values (Conley & Krahenbul, 1980).

Altering RE by adding mass to the shoes has been shown to directly translate to altered endurance running performance over 3000 m (Hoogkamer et al., 2016). Furthermore, recent advances in footwear technology (Hoogkamer et al., 2018) have been driven by the idea of improving RE to improve performance times. Kipp et al. (2019) modelled that the current Marathon world record holder, Eliud Kipchoge, who had a previous personal best of 2:04:00 h, would require a 3% improvement in RE to run his current world record (2:01:39 h). This improvement in RE may have been provided solely by the shoes, which reportedly improve RE by 4% (Hoogkamer et al., 2018), although the exact magnitude of improvement that Kipchoge receives from the shoes is not known (Kipp et al., 2019).

Factors Influencing Running Economy

Running economy is influenced by many anthropometrical, biomechanical and physiological variables (Barnes & Kilding, 2015b; Saunders et al., 2004). Body mass and its distribution are some of the anthropometrical variables that influence RE. Cr does not increase proportionally to body mass (Pate et al., 1992) and it has been shown that adding weight to the trunk to artificially increase body mass decreases O_2C per kg of mass displaced (Abe et al., 2011; Cooke et al., 1991; Thorstensson, 1986), and several studies have shown a small to moderate inverse relationship between body mass and RE (Pate et al., 1992; Williams & Cavanagh, 1987). The distribution of the body mass also seems to be important, with a higher percentage of mass located closer to the center of gravity having a lower impact on RE. For example, long and thin limbs, with most of the mass of the legs located in the thigh, as opposed to the lower leg, has been suggested to be a main reason for the better RE of African runners (Lucia et al., 2006; Wilber & Pitsiladis, 2012). This is supported by other experiments which have added the same mass to different body segments of runners, indicating that RE worsened more when the mass was placed more distally (Jones et al., 1986; Martin, 1985; Myers & Steudel, 1985). For example, it was found that carrying an extra kilogram on the trunk increased CO by 1%, while adding 1 kg to the shoes

increased CO by 10% (Myers & Steudel, 1985). This suggests that foot size as well as shoe choice can have an impact in RE. Other anthropometric characteristics seem to influence RE. The moment arm of the Achilles tendon is related to RE, with longer moment arms related to higher $\dot{V}O_2C$ (Barnes et al., 2014; Raichlen et al., 2011; Scholz et al., 2008).

Different biomechanical variables have an important impact on RE. Stride length and stride rate influence RE, with several studies showing that $\dot{V}O_2$ increases for the same running speed when stride length is lengthened or shortened compared to self-selected stride length (Cavanagh & Williams, 1982; Hogberg, 1952; Knuttgen, 1961; Powers et al., 1982). It has been suggested that runners tend to self-optimize stride length and rate over time, based on their perceived exertion (Williams & Cavanagh, 1987), and that runners may adapt to a particular stride length and rate for a given running speed as they repeat it during training (Cavanagh & Williams, 1982). Vertical oscillation is another possible variable that may influence RE since, theoretically, more vertical oscillation could require more force being used to propel the body upwards, instead of forward, therefore decreasing the amount of force that is converted to horizontal speed. Several studies have compared the biomechanics of elite vs good runners and found that elite runners have less vertical oscillation, as well as better RE, than good runners (Cavagna et al., 2005; Cavanagh et al., 1977; Tartaruga et al., 2012), while Williams and Cavanagh (1987) showed a nonsignificant trend towards less vertical oscillation and better RE, and Halvorsen et al (2012) reported improved Cr through a reduction in vertical oscillation. However, Cavagna et al (2005) reported that lower vertical oscillation led to higher stride frequency and higher internal work, increasing O_2 demand and worsening RE. Footstrike pattern has also been argued to affect RE. In cross-sectional studies, the relationship between footstrike pattern and RE may be affected by the fact that high-level runners are less likely to be heel strikers (Kasmer et al., 2013). However, previous studies have shown no effect of footstrike pattern on runners who were using their habitual footstrike (Di Michele & Merni, 2014; Gruber et al., 2013) while, when changing footstrike pattern to their unhabitual pattern, $\dot{V}O_2$ increased significantly with the forefoot pattern, but not with the rearfoot pattern, suggesting that a forefoot pattern is not more economical (Gruber et al., 2013).

Several physiological factors have been shown to influence RE (Barnes & Kilding, 2015b). These include temperature, cardiorespiratory factors, and muscle fiber type. Pate et al. (1992) reported, in a sample of 188 habitual runners, that O_2C correlated significantly with HR and \dot{V}_E .

Myocardial and ventilatory work have been shown to account for up to 1-2% and 7-8% of the overall energy cost of exercise (Bailey & Pate, 1991; Coast et al., 1993; Coast & Krause, 1993; Kitamura et al., 1972). However, this does not necessarily mean that the work of the heart and the ventilatory muscles is the cause of higher $\dot{V}O_2$ during exercise, since it is also possible that a greater O_2 demand during exercise elicits a greater cardiorespiratory response. Regarding muscle fiber type, it is well known that humans possess a range of fiber types (Williams & Cavanagh, 1987) generally classified as type I fibers, with greater oxidative capacity and fatigue resistance, and type II, less fatigue resistant and less oxidative and with a greater preference for anaerobic energy production. type II fibers are divided in type IIA and type IIX, and type IIA fibers have intermediate characteristics between type I and type IIX. Muscle fiber composition seems to influence RE (Kaneko, 1990; Kyrolainen et al., 2003; Morgan & Craib, 1992). The myosin ATPase isoforms present in type II fibers require 1.6 to 2.1 times more ATP per unit of force production than type I, which in turn creates a proportionally higher oxygen demand (Reggiani et al., 2000). Therefore, a greater proportion of type I fibers should contribute to a lower Cr. However, current research is not clear, and there are mixed findings between muscle fiber type and RE (Bosco et al., 1987; Kaneko, 1990; Heikki Kyrolainen et al., 2003; Williams & Cavanagh, 1987). The relationship between fiber type and efficiency seems to be clearer in cycling, with studies showing strong correlations between greater efficiency and greater percentage of type I muscle fibers (Coyle et al., 1992; Horowitz et al., 1994).

RE can be improved through several training interventions (Barnes & Kilding, 2015a). Elite trail runners tend to have better running economy than runners of lower level. Therefore, the number of years of running training experience, as well as high training volumes have been suggested to be associated with better running economy (Daniels et al., 1978; Nelson & Gregor, 1976). However, the few longitudinal studies that have examined the effect of training experience and volume have found varying results, including no changes (Daniels et al., 1978; Wilcox & Bulbulian, 1984), or reductions ranging from 1-15% (Conley et al., 1981; Patton & Vogel, 1977; Sjödín et al., 1982; Svedenhag & Sjödín, 1984) in submaximal O_2C . It has been suggested that the most important factor to improve RE may be the cumulative distance that a runner has run over several years, and not the volume of running in the short term, like recent months or a recent training block (Midgley et al., 2007). Case studies world-class runners also suggest that RE improves over several years (Conley et al., 1984; Ingham et al., 2012; Jones, 2006). However,

longitudinal studies on the effect of running training volume over the long term on RE are needed before reaching conclusions about their effect on RE. The other main training intervention that has been studied to promote improvements in running economy is resistance training. Resistance training has showed to improve RE in recreational (Hickson et al., 1988; Taipale et al., 2010, 2013), moderately trained (Guglielmo et al., 2009; Johnson et al., 1997; Støren et al., 2008) and highly trained runners (Millet et al., 2002; Sedano et al., 2013). There are several mechanisms through which resistance training may improve RE, including improvements in lower limb coordination and co-activation of muscles (Kyröläinen et al., 2001), decreased motor unit activation to produce a given force (Moritani & deVries, 1979), and improvements to the nervous system allowing increased activation of the working muscles (Sale, 1988). Plyometric training has also shown to improve running economy, through improvements in the stiffness of the muscle-tendon system and the stretch-shortening cycle, leading to decreased ground contact time and energy expenditure (Paavolainen et al., 1999; Saunders et al., 2006; Spurrs et al., 2003).

It is well known that the incline has an important influence on RE (Breiner et al., 2019; Lemire et al., 2021). During uphill running the body's center of mass must be elevated as it is moved forward, resulting in an increase in mechanical work performed (Margarita et al., 1963; Minetti et al., 2002), and therefore an increase in Cr for a given running speed or a reduced speed for a given Cr. Concentric muscle contractions, which have a higher metabolic cost, are predominant during uphill running, which might shift the emphasis of RE towards metabolic factors. During downhill running there is less requirement for concentric work from the muscles, as well as an increase in vertical velocity during landing, which leads to greater energy storage and re-utilization during each step (Fletcher & MacIntosh, 2017), leading to decreased Cr for a given speed (Margarita et al., 1963; Minetti et al., 2002). This may potentially shift the emphasis to biomechanical factors related to tendon stiffness as the main determinants of downhill RE. Minetti et al. (2002) found that the optimal gradient to minimize Cr during running was -20%, which was 49% lower than Cr during level running. Deviating from that gradient in either direction increased Cr, with Cr being 15% greater at -45% gradient than during level running, and 560% greater at +45% incline compared to level running (Figure 15).

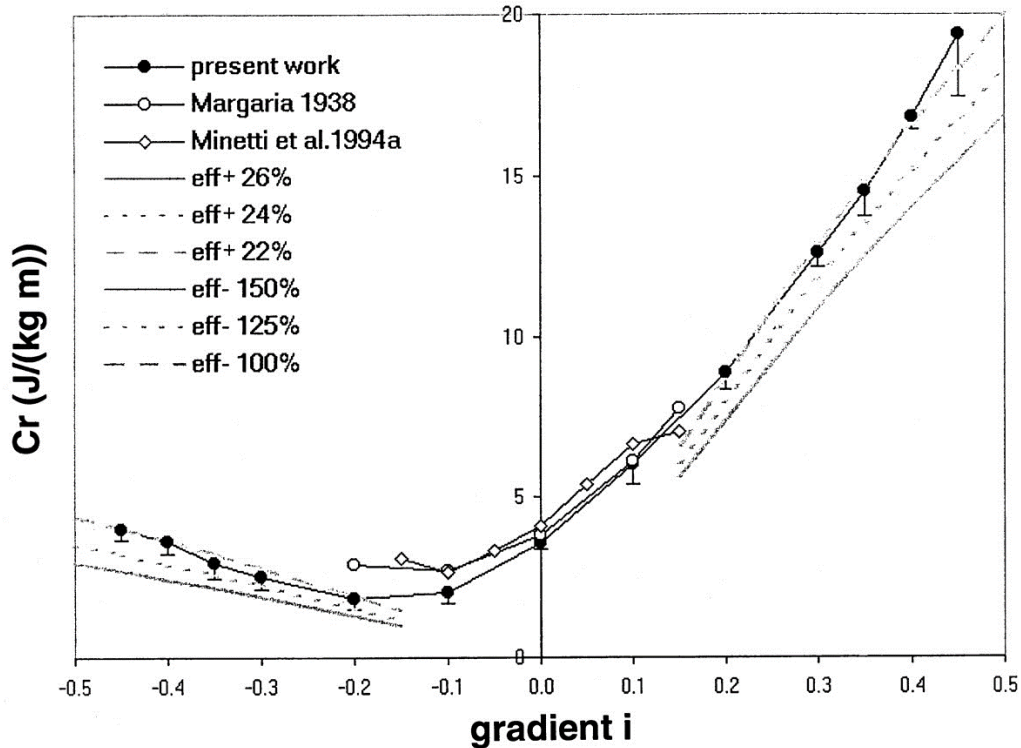


Figure 15. Metabolic Cr of running as a function of the gradient (in radians). Data from different experiments by Margaria (1938; 1963) and Minetti (1994, 2002) are included. From Minetti et al. (2002).

Assessment of running economy

In exercise modalities in which mechanical power can be accurately measured, such as cycling, exercise economy is commonly measured as efficiency, the ratio of mechanical work produced over metabolic energy consumed. However, since power is difficult to measure accurately during running exercise, O_2C has been used as the measure of RE for decades (Jones, 2006; Lucia et al., 2006; Pate et al., 1992; Pollock, 1977; Williams & Cavanagh, 1987), assuming that O_2C is a good surrogate of Cr when the aerobic metabolism can supply all of the energetic needs for exercise (Fletcher & MacIntosh, 2017). This has led to the use of the terms O_2C and Cr interchangeably by some authors. However, recent evidence (Fletcher et al., 2009; Shaw et al., 2014) has shown a discrepancy between changes in O_2C and Cr with changing speed, which suggests that O_2C may not be a valid measure of Cr.

Oxygen cost has been reported to be constant across a range of running speeds for the same subjects (di Prampero et al., 2009; Hagberg & Coyle, 1984). However, Cr has been shown to

increase in relation to increases in speed, while O_2C remained constant (Fletcher et al., 2009; Shaw et al., 2014). The disparity between O_2C and Cr is probably caused by the different energy yield of O_2 as the energy substrates for oxidations shift from lipids to carbohydrates (CHO) with increasing exercise intensity. It is well known that the energy yield of CHO (5.02 kcal/L) is greater than lipid (4.85 kcal/L) oxidation (Péronnet & Massicotte, 1991). As a consequence of this, the O_2 demand of a task depends on the relative contribution of each substrate, which can be assessed through the respiratory exchange ratio (RER). RER has consistently been shown to increase as exercise intensity increases, reflecting an increase in CHO oxidation at higher intensities (Fletcher et al., 2009; Shaw et al., 2014), which is associated with higher energy yield per unit of oxygen. Therefore, it is possible that the increase in energy yield of oxygen may be similar in magnitude to the increase in energy demand, keeping O_2C constant while running speed and Cr increase. Because of this, Cr seems to be a better measure of RE, and it should be expressed in units of energy used per unit of body mass and per distance covered (J/kg/m or kcal/kg/km).

Another important aspect for the assessment of RE is the intensity at which the measurement is performed. Since the measurement assumes $\dot{V}O_2$ to be reflective of total energy demand, it is necessary to exercise at an intensity below the second threshold, because at greater intensities there is a part of the energy that is provided by anaerobic energy sources and unaccounted for by $\dot{V}O_2$ (Svedahl & MacIntosh, 2003). Beyond the second threshold there is a slow component of $\dot{V}O_2$, and $\dot{V}O_2$ increases despite sustained exercise intensity. This phenomenon does not allow the possibility of assuming a correspondence between running speed and $\dot{V}O_2$, since $\dot{V}O_2$ is constantly changing while running at those intensities. Therefore, an intensity below the second threshold is required, as well as sufficient time to allow the slow component to stabilize if exercise is performed in the heavy domain. Otherwise, O_2C , and therefore Cr, could be underestimated.

The slope of the treadmill must also be considered when measuring RE, especially in trail runners. During treadmill running there is no effect of air resistance, due to the lack of horizontal displacement. Because of this, it has been suggested that treadmill testing should be performed at a 1% incline, to compensate through the incline for the lack of air resistance (Jones & Doust, 1996). In the case of trail runners, the incline at which RE is measured seems especially relevant, since trail runners compete in steeper slopes. However, it seems that there is a strong correlation

between Cr measured during level treadmill running and downhill running up to at least -5% slopes ($r = 0.901$, $p < 0.01$, (Breiner et al., 2019) and uphill at 7.5% ($r = 0.909$, $p < 0.01$, (Breiner et al., 2019)) to 12% incline ($r=0.826$, $p < 0.01$, (Willis et al., 2019)) in well trained runners who encounter hills during their training in a regular basis. These results may appear to suggest that the slope is irrelevant when testing Cr of trail runners. However, other research has shown that the relationship between Cr values at different inclines is lost at steeper slopes. Lemire et al. (2021) tested 29 participants at different slopes, ranging from -20% to +20 % in increments of 5%, except at -15%. They found strong correlations between Cr at all incline combinations except at level vs +20%, and -20% vs +20%, suggesting that Cr at greater inclines is influenced by different mechanisms than Cr during level running. The authors suggested that the lack of correlation at steep slopes may be due to the increased concentric work at steep slopes, whereas at lower slopes the stretch-shortening cycle is of more importance. However, the authors also recognized that only 6 subjects were able to complete the 20% incline test, which decreased the statistical power of their correlation analysis at that steep slope. Other evidence suggesting that uphill Cr may be relevant for trail runners is the study of Ehrstrom et al. (2018) which found that level Cr was not a predictor of performance in a 27 km trail running race, whereas uphill Cr was.

Running economy and trail running performance

Two studies found a correlation between running economy, measured either during flat treadmill running or uphill treadmill running, and performance in trail running races from 27 to 75 km (Ehrström et al., 2018; Scheer, Janssen, et al., 2019). However, other studies have failed to find a relationship between Cr and trail running performance (Balducci, Cléménçon, et al., 2017; Björklund et al., 2019; Coates et al., 2021). It has been suggested that running economy may be of less importance in trail running in ultramarathon distances when compared to road running (Millet et al., 2012). This may be due to the fact that some strategies that may increase Cr, such as wearing heavier and more cushioned shoes, or carrying hiking poles, are widely used by trail runners, with the goal of decreasing the impact on the legs, therefore decreasing damage to the muscle, tendons and joints, as well as fatigue of the locomotor muscles. It is possible that these strategies are used because the performance consequences of greater damage, including having to decrease speed or even having to retire from the competition due to pain, outweigh the possible advantage of trying

to be more economical, for example by carrying less equipment and therefore less weight (Millet et al., 2012).

3.2.4. Other factors affecting performance in trail running

Several studies have suggested that the classical model of endurance running performance, including $\dot{V}O_2\text{max}$, fractional utilization and running economy, does not apply to trail running (Alvero-Cruz et al., 2019; Ehrström et al., 2018; Fornasiero et al., 2018; Gatterer et al., 2020). This suggests that there may be other factors that will significantly influence performance in trail running, which are either not so relevant for road running or strongly correlated with the three main factors, which makes them not relevant by themselves during road running, but their effect may be greater during trail running. One example of this may be body composition. Body fat percentage is negatively associated with $\dot{V}O_2\text{max}$, (Mondal & Mishra, 2017) since $\dot{V}O_2\text{max}$ is usually calculated relative to body mass, and a higher fat content increases mass, while contributing negligibly to oxygen uptake. This may be accounted for during flat running with the measure of $\dot{V}O_2\text{max}$, but it is possible that for trail running, due to the elevation gains and losses during the race, body fat percentage may be associated with performance independently from $\dot{V}O_2\text{max}$. Indeed, several studies have found relationships between body composition and trail running performance, assessing variables such as body fat percentage (Alvero-Cruz et al., 2019; Björklund et al., 2019; Fornasiero et al., 2018) and body mass index (Alvero-Cruz et al., 2019; Fornasiero et al., 2018). Furthermore, Fornasiero et al. (2018) found that body fat percentage and body mass index were both related to performance independently of $\dot{V}O_2\text{max}$ in a 65 km trail race. Body composition is also important for road running. It has been shown that male and female elite runners have lower body fat than their non-elite counterparts (Bale et al., 1986; Bale et al., 2007). Pollock et al. (1977) measured body fat in elite track and marathon runners using the underwater weighing technique and found that middle- and long-distance track runners had a fat mass equivalent to $5.0 \pm 3.5\%$ of body mass, while for marathon runners it was $4.3 \pm 3.0\%$. Furthermore, lower body fat was a significant predictor of performance in 1353 women and 1771 men running a 4.8 or 7.2 km race (Herrmann et al., 2019).

Neuromuscular factors in trail running have been extensively researched in relationship to fatigue, but their relationship with race performance has not been widely studied. Due to the inclines during trail running races, it is possible that trail running has increased strength demands

compared to road running in the extensor muscles of the legs, since they must work concentrically to carry the athlete's mass during the uphill sections and eccentrically to slow down and absorb forces during downhill sections. The different studies that have taken neuromuscular performance of the legs into consideration to explain trail running performance have used different methods. Balducci et al. (2017) assessed maximal isometric strength of the knee extensor as well as a countermovement jump and found a significant correlation between maximal voluntary contraction (MVC) and performance time ($r = -0.51$), but no relationship with countermovement jump height in a 75 km race. Ehrström et al. (2018) measured knee extensor MVC in concentric and eccentric mode, as well as a fatigue index, calculated as the loss in force during 40 MVC repetitions. They found no relationship between performance in the concentric or eccentric MVC, but the fatigue index was the most important predictor in a model of trail running performance. The fatigue index explained 49.8% of the variability and was a performance predictor independently of $\dot{V}O_2\text{max}$ and uphill Cr, suggesting that muscular endurance is an important determinant of performance in trail running. Finally, Baiget et al. (2018) used a countermovement jump as well as repeated jumps during 15 seconds as their measures of neuromuscular performance. They found an association between the mean height during the repeated jumps and performance in a 21.1 km trail race, and mean height during the repeated jumps post-race was a significant predictor of performance.

Another factor that may be influential for trail running performance is fuel utilization. Considering the duration of most trail running races exceeds two hours, it is very likely that trail runners will benefit from improved lipid oxidation at race intensity. To regenerate ATP aerobically there are two main fuels that can be used, lipids and CHO, as well as a small amount of protein. CHO is stored in the body in two main forms: as glycogen in the muscles and the liver and as free glucose in the blood. The human body stores up to around 400 g of glycogen in the muscle and 100 g in the liver, which amount to a total of around 2,000 kcal. Since trail runners will often race at intensities requiring more than 500 kcal/h, even more than 1,000 kcal/h in the case of elite athletes, and races can last for multiple hours, it is clear that the CHO stores in the body are not enough to complete the events, since glycogen depletion in the muscles has been associated to failure in excitation-contraction coupling of the muscles (e.g. Ørtenblad et al., 2013). Therefore, athletes are required to provide exogenous CHO during exercise. Current recommendations suggest ingesting 60-90 g/h of CHO during endurance exercise (Jeukendrup, 2014), and CHO

intakes up to 120 g/h have been used in experimental settings with trail runners during a mountain marathon (Viribay et al., 2020), suggesting that these greater intakes may contribute to diminishing muscle damage during trail running races. However, this CHO intake is still not sufficient to provide all the energy to complete trail running races lasting multiple hours, and higher CHO intakes are associated with gastrointestinal distress, which may be detrimental for performance, requiring even abandoning the competition in some cases. Therefore, it could be advantageous for trail runners to be able to oxidize more lipids at any given intensity, and especially at race intensities, allowing them to have a lower rate of glycogen depletion, since a higher percentage of the energy is produced via fat oxidation. Indeed, one study has assessed the impact of fat oxidation ability on trail running performance, finding maximal fat oxidation (the highest measured rate of fat oxidation, measured in grams per hour, during an incremental test) was a determinant of performance in a race of 107 km (Martinez-Navarro et al., 2020). Splitting the results by sex, they found that maximal fat oxidation was a predictor of performance for men, but not for women, despite a significant correlation with performance for women as well. Maximal fat oxidation has also been shown to predict performance in other long-duration sports, such as Ironman triathlon (Frandsen et al., 2017; Vest et al., 2018). The effect of fat oxidation race in middle-distance and long-distance running performance has not received much attention in the literature. However, it has been shown that higher maximal fat oxidation levels are observed in elite cyclists compared to recreationally trained cyclists (San-Millán & Brooks, 2017) and fat oxidation rates at the same intensity relative to $\dot{V}O_2\text{max}$ were higher in trained cyclists compared to untrained subjects (van Loon et al., 1999).

To better understand what are the performance factors in trail running, two studies were conducted as part of the doctoral project. Study 1 aimed to test for differences between elite road and trail runners in some selected performance factors. This would allow us to better understand the factors that may be more beneficial for each discipline. Study 2 was performed with the goal of identifying the performance determinants of trail running races of different distances, ranging from 40 km to 170 km. Since the physiological demands of trail running races vary depending on the distance, we aimed to identify potential differences in the factors that affect performance across a range of race distances.

3.3. Elite road vs. trail runners: comparing economy, biomechanics strength, and power (Study 1).

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Introduction

During recent decades, trail running has seen an increase in popularity and participation compared to road running. (Ronto, n.d.) Despite the increasing popularity of trail running, the best elite road and track runners in the world have not transitioned to trail racing. Moreover, elite athletes in each discipline are different, with no elite runners participating and achieving success at the same time in elite international competitions in both disciplines. This may be related to social and economic factors. For example, trail running tends to have less "prize money" and it is not an Olympic sport. (Huber, 2019) However, it is also possible that elite road runners are not "well-suited" for the specific physiological or biomechanical demands of trail running. To the best of our knowledge, the physiological and biomechanical differences between trail and road runners have not been previously studied. The different physiological and biomechanical demands of road and trail running races could be the reason why different athletes succeed in each discipline. Road running races are normally events of 10 km to the marathon distance, ran on asphalted roads, and with small elevation changes. For instance, the six World Marathon Majors range in elevation gain from 74 to 260 m. In contrast, trail running races include varying terrains as well as positive and negative elevation changes. (Scheer et al., 2020) For example, the 2019 Trail World Championship was run over 44.2 km with 2120 m of elevation gain. (International Trail Running Association, n.d.) The environment in which trail running races are run may require specific biomechanical adaptations. The terrain in which trail running races are run can vary from hard rock to soft terrain. The characteristics of the terrain of trails, together with the changes in elevation, lead to lower running speeds during training and competition, compared to road running.

The classical model for running performance prediction includes maximal oxygen uptake ($\dot{V}O_{2max}$), the fractional utilisation of $\dot{V}O_{2max}$, and cost of running (Cr) (Joyner & Coyle, 2008). A case study showed that the former female world record holder in the marathon improved her

performance along with her Cr over a period of 10 years leading to her record, with no changes of $\dot{V}O_2\text{max}$ during that period (Jones, 2006), and the lowest Cr ever reported was measured on a former world record holder in the half marathon (Lucia et al., 2008). A few studies have investigated the factors that influence performance in trail running finding an influence of physiological parameters such as $\dot{V}O_2\text{max}$ and the velocity at $\dot{V}O_2\text{max}$ (Balducci, Cl  men  on, et al., 2017; Ehrstr  m et al., 2018), as well as lactate thresholds (Scheer, Vieluf, et al., 2019). Cr has also been identified as a performance factor in trail running. Ehrstrom et al. (2018) found that uphill cost of running (Cr_{UH}) predicted trail running performance, while flat cost of running (Cr_{FLAT}) did not. However, other studies have not found a relationship between Cr_{FLAT} or Cr_{UH} and trail running performance (Balducci, Cl  men  on, et al., 2017). Cr has been shown to improve at the specific speed at which runners train (Jones & Carter, 2000), and it is possible that the same applies for slope. Therefore, trail running training may improve Cr_{UH} more than Cr_{FLAT} , while road running will lead to greater improvements in Cr_{FLAT} , especially at higher speeds. Furthermore, running economy is influenced by biomechanical parameters such as running kinematics, including step length and frequency, (Cavanagh & Williams, 1982; Halvorsen et al., 2012) and by vertical and leg stiffness (Moore et al., 2019), and it is not known if these biomechanical parameters are different in road compared to trail runners.

The elevation changes during trail running races may require specific neuromuscular adaptations compared to road running, especially in the extensor muscles of the lower limbs, to propel the athlete during the uphill sections (Padulo et al., 2013). Therefore, it seems that a thorough assessment of the variables that may differentiate road and trail runners should include strength and power testing, since knee extensor strength has been shown to predict performance in trail runners (Balducci, Cl  men  on, et al., 2017; Ehrstr  m et al., 2018). However, those studies have only assessed strength during isolated knee extension exercise, which may be too different from the dynamic movements involved in running, and therefore they may not reflect the strength that an athlete is able to produce during dynamic exercise. The Force-Velocity Profile (FVP) has been proposed as a method to assess force production capacity, as well as velocity of movement and power production during dynamic exercise (Cross et al., 2017; Jim  nez-Reyes et al., 2017). It has been used to assess force and power in athletes, including recreational marathon runners, finding that higher force and power values are negatively related to marathon performance (Nikolaidis & Knechtle, 2020).

To date, no study has directly compared the differences in terms of Cr, running biomechanics, strength, and power between trail and road runners. The purpose of this study is to test for differences in strength and power production capacity, Cr, biomechanics (including running kinematics and stiffness), and training between road vs trail elite runners. It was hypothesised that, compared to road runners, trail runners would i) be more powerful and have a more force-oriented force-velocity profile, ii) have higher levels of isometric strength, iii) have a better Cr_{UH} but worse Cr_{FLAT} .

Methods

Experimental Approach to the Problem

A cross sectional experiment design was used to compare the differences between trail and road elite runners. Elite road and trail runners, which were required to be selected for the French national team for inclusion, were compared. The neuromuscular performance was compared during dynamic muscle contractions with an FVP using a two-sprint test on a bicycle ergometer, as well as during isometric contractions. Cr was calculated while running at submaximal intensities on a treadmill on flat and uphill conditions and spatiotemporal step variables were measured during the treadmill test to assess differences in running biomechanics. Athletes reported their average training duration per month over the previous year using a questionnaire. All data are presented as mean \pm SD.

Subjects

Seventeen elite male athletes, 7 road runners (ROAD, age 27.0 ± 4.8 years, body mass 62.6 ± 3.9 , height 177.1 ± 6.7) and 10 trail runners (TRAIL, age 30.8 ± 8.3 years, body mass 65.6 ± 5.6 , height 176.7 ± 6.7). All participants in this study were members of the French national team in their respective disciplines, and were invited to training camps with the national team. The athletes were tested during their training camps with the national federation. Road runners had an average best 10 km time of 29:17 min [range 28:06–30:56]. Trail runners had an average performance index of 864 points [range 852-901] according to the International Trail Running Association, and included the members of the teams that won the 2019 Trail World Championship and obtained 4th place at the 2019 World Mountain Running Championships. According to the

International Trail Running Association the trail runners were classified in the Elite 2 category or better, being among the highest ranked 268 trail runners in the world. The study obtained approval from the local ethics committee and all athletes provided their written informed consent to participate.

Procedures

Force-Velocity Profile

After a brief warm-up, participants sat on a cycle ergometer (Monark, Vansbro, Sweden) equipped with a strain gauge (FGP Instrumentation, FN 3030 type, Les Cloyes Sous Bois, France) and an optical encoder (Hengstler type RI 32.0, 100 pts/turn, Aldingen, Germany) which measured friction force and flywheel displacement, respectively. Torque at the pedal and angular velocity of the crank were calculated from the measured force and linear displacement. Each participant performed two eight-second all-out seated sprints from a stationary sitting start on the ergometer against friction loads of 0.5 N/kg and 0.7 N/kg respectively, with 2 minutes of rest between sprints. Force, velocity and power were measured for each pedal stroke and the parameters of the force velocity relationship were calculated (Samozino et al., 2007). The theoretical maximal force (F_0), the theoretical maximal velocity (v_0) and the maximal power, (P_{\max}) calculated as:

$$P_{\max} = F_0 \times v_0 / 4$$

F_0 and P_{\max} were also expressed relative to body mass. Since v_0 and F_0 express the absolute velocity and force capacity of the athletes independently from the specific loads used for testing, we reported and analysed these variables instead of the more load-dependent maximum force and maximum velocity measured.

Isometric Strength

Participants sat in an upright position on a custom-built chair which kept knee and hip angles at 90°. Their leg was attached to a force transducer (Meiri F2732 200 daN; Celians, Montauban, France) proximal to the medial malleolus using a noncompliant strap. After 5 submaximal warm-up contractions, participants performed two 4-second maximal voluntary contractions (MVC) of knee extension (KE) and knee flexion (KF), while strong verbal encouragement was provided. Both legs were measured, and the highest force produced was taken

as for each leg. The force value was then multiplied by the moment arm (i.e. the length from the center of rotation of the knee and the line of action) to obtain the torque value. Afterwards, both legs were averaged to obtain a single value for KE and KF, respectively, which was normalized to body mass.

Cost of Running

Participants ran 3 bouts of 4-min on a calibrated treadmill in three different conditions: two flat conditions, at 10 km/h (FLAT10) and 14 km/h (FLAT14), and an uphill condition at 10 km/h at 10% incline (UH). Participants were equipped with a portable gas exchange analyzer (Metamax 3B, Cortex, Leipzig, Germany) which measured oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$). Those data were used to calculate Cr using the combination of $\dot{V}O_2$ and the energy equivalent of O₂ based on the respiratory exchange ratio (Péronnet & Massicotte, 1991).

Biomechanical Measures

During the last minute of each 4-min testing period of the Cr test, 30 s of ground contact time and flight time were collected using an optical measurement system (Optojump Next, Microgate, Bolzano, Italy). Contact time and flight time were used to calculate step frequency and duty factor. Leg stiffness and vertical stiffness were calculated using running speed, contact time, flight time and participant mass and height (Morin et al., 2005).

Training and Competition Data

Subjects answered a questionnaire reporting their training and competition data during the previous year. They reported the number of competitions as well as the discipline (trail, road, track and cross country), and the average monthly training hours for each training modality (road, track and trail running, aerobic cross-training such as swimming or cycling, and resistance training).

Statistics

All measured variables were tested for normality using the Shapiro-Wilk test. If the data met the assumption of normality, both groups, trail and road, were compared using an independent samples *T*-test. If the assumption of normality was not met, the groups were compared using a Mann-Whitney non-parametric test. Data are reported with 95% confidence intervals (CI) and Cohen's *d* for effect size. Significance was established at a level of $p < 0.05$.

Results

Subject Characteristics

No significant differences between groups were found in terms of age, body mass and height.

Force-Velocity Profile

F_0 was significantly higher in TRAIL compared to ROAD ($p < 0.001$, 95% CI [11.12, 34.84], $d = 2.04$) while no differences in v_0 were found between the two groups (Figure 16). Maximal power was higher in TRAIL compared to ROAD (726 ± 89 vs 626 ± 44 W, $p = 0.016$, 95% CI [21.61, 178.09], $d = 1.34$). Accounting for body mass, TRAIL still had higher F_0 than ROAD (1.87 ± 0.18 vs 1.57 ± 0.11 N·m/kg, $p = 0.002$, 95% CI [0.132, 0.465], $d = 1.89$), while the difference in relative maximal power did not reach the level of significance (11.1 ± 1.2 vs 10.0 ± 0.8 W/kg, $p = 0.065$, 95% CI [-0.075, 2.207], $d = 0.98$).

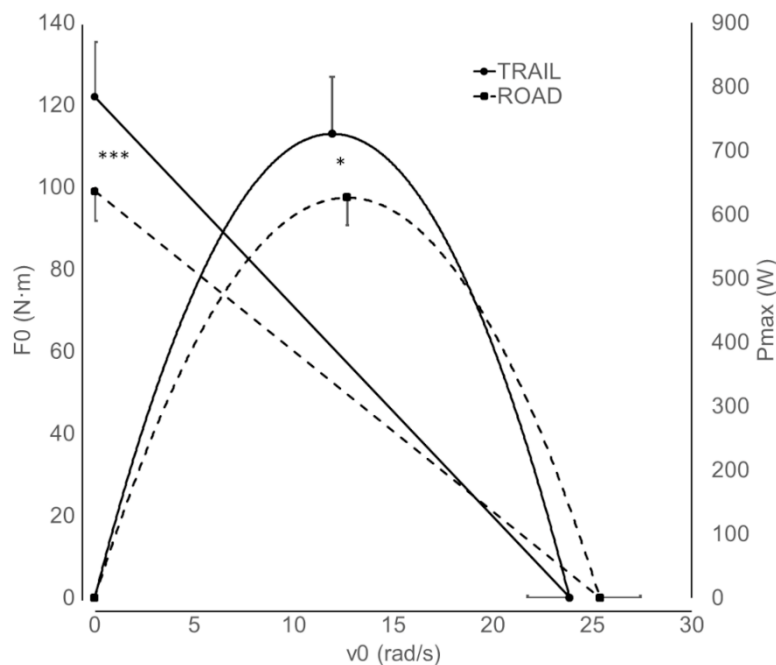


Figure 16. Mean force-velocity profile (straight lines) and power-velocity profile (parabolic lines) of elite TRAIL and ROAD runners. Difference between road and trail runners: *** $p < 0.001$, * $p < 0.05$.

Isometric Strength

There were no differences between TRAIL and ROAD in KE or KF absolute isometric torque or torque relative to body mass measured as the average of the two legs (Table 3). No significant differences between TRAIL and ROAD were obtained when assessing each leg separately.

Table 3. Isometric torque characteristics of elite TRAIL and ROAD Runners.

	TRAIL	ROAD
Absolute KE (N·m)	199.3 ± 55.4	164.3 ± 16.6
Relative KE (N·m/kg)	3.07 ± 0.78	2.64 ± 0.36
Absolute KF (N·m)	62.7 ± 16.0	55.4 ± 7.8
Relative KF (N·m/kg)	0.95 ± 0.19	0.89 ± 0.15

KE: knee extensors, KF: knee flexors.

Cost of Running

$C_{r_{FLAT14}}$ was significantly higher in TRAIL compared to ROAD (4.32 ± 0.22 vs 4.06 ± 0.29 J/kg/m, $p = 0.047$, 95% CI [0.004, 0.522], $d = 1.07$, Figure 17) but the difference did not reach the level of significance for $C_{r_{FLAT10}}$ (4.37 ± 0.27 vs 4.09 ± 0.31 J/kg/m, $p = 0.064$, 95% CI [-0.019, 0.587], $d = 0.99$). $C_{r_{UH}}$ was not different in TRAIL compared to ROAD either (6.76 ± 0.22 vs 6.64 ± 0.42 J/kg/m, $p = 0.461$, 95% CI [-0.066, 0.01], $d = -0.778$). However, $C_{r_{FLAT10}}$ was related to $C_{r_{FLAT14}}$ when considering pooled data as well as when separating the data in TRAIL and ROAD.

Biomechanical Parameters

As shown in Table 4, there were no differences between TRAIL and ROAD in flight time, contact time, step frequency, duty factor, leg stiffness and vertical stiffness in any of the three conditions.

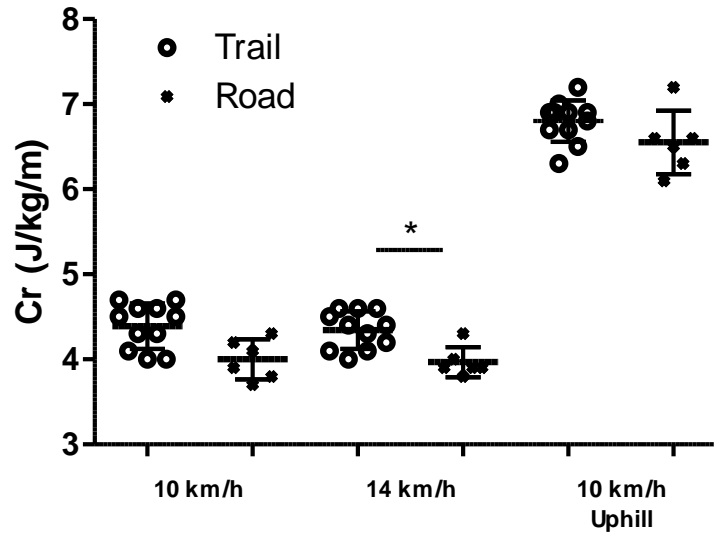


Figure 17. Cost of running of elite TRAIL and ROAD runners. Difference between road and trail runners: * $p < 0.05$.

Table 4. Biomechanical parameters of road and trail runners during flat 10 and 14 km/h running and during 10 km/h at 10% incline.

		FLAT10	FLAT14	UH
FT (ms)	TRAIL	52 ± 20	99 ± 15	49 ± 17
	ROAD	62 ± 24	99 ± 21	55 ± 19
CT (ms)	TRAIL	309 ± 29	249 ± 20	309 ± 28
	ROAD	301 ± 21	250 ± 11	303 ± 13
SF (Hz)	TRAIL	2.78 ± 0.15	2.88 ± 0.13	2.80 ± 0.14
	ROAD	2.76 ± 0.12	2.88 ± 0.13	2.81 ± 0.13
DF (%)	TRAIL	85.6 ± 5.6	71.6 ± 4.3	86.3 ± 4.8
	ROAD	83.0 ± 6.3	71.8 ± 4.9	84.9 ± 4.9
K _{Leg} (kN/m)	TRAIL	7.42 ± 1.23	7.37 ± 1.14	7.42 ± 1.20
	ROAD	7.46 ± 0.94	6.97 ± 0.82	7.33 ± 0.63
K _{Vert} (kN/m)	TRAIL	21.00 ± 1.77	24.06 ± 2.14	21.30 ± 1.66
	ROAD	19.91 ± 0.91	22.90 ± 1.12	20.40 ± 1.21

FT, flight time; CT, contact time; SF, step frequency; DF, duty factor; K_{Leg}, leg stiffness; K_{Vert}, vertical stiffness.

Training and Competition

Total training duration was higher for ROAD compared to TRAIL (79.0 ± 20.5 vs 43.6 ± 10.6 h/month, $p < 0.001$, 95% CI [51.49, 19.31], $d = 2.31$). The duration of total endurance training, including cross-training, running training and resistance training was significantly greater in ROAD compared to TRAIL (Figure 18). There were no significant differences in the total number of yearly competitions between TRAIL and ROAD (

Table 5).

	Trail Races	Road Races	Athletics Races	Total Races
TRAIL	9.8 ± 2.4	0.2 ± 0.4	2.8 ± 3.2	12.8 ± 4.8
ROAD	$0.4 \pm 1.1^{***}$	$10.7 \pm 8.3^{***}$	$6.0 \pm 2.2^*$	17.1 ± 6.2

Significantly different from TRAIL: * $p < 0.05$; *** $p < 0.001$. Athletics races include track events and cross-country races.

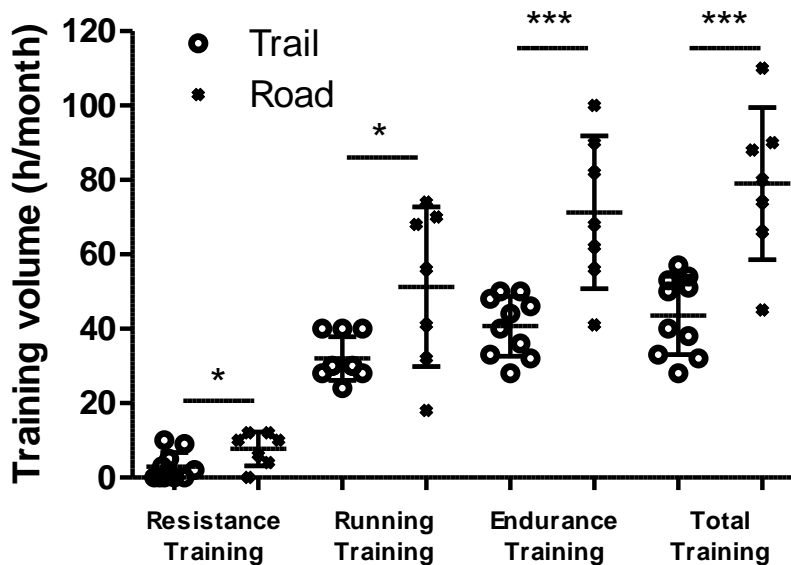


Figure 18. Monthly training hours of elite TRAIL and ROAD runners. Difference between road and trail runners: * $p < 0.05$; *** $p < 0.001$.

Table 5. Number of races competed per year by elite ROAD and TRAIL runners.

	Trail Races	Road Races	Athletics Races	Total Races
TRAIL	9.8 ± 2.4	0.2 ± 0.4	2.8 ± 3.2	12.8 ± 4.8
ROAD	0.4 ± 1.1***	10.7 ± 8.3***	6.0 ± 2.2*	17.1 ± 6.2

Significantly different from TRAIL: * $p < 0.05$; *** $p < 0.001$. Athletics races include track events and cross-country races.

Discussion

The main findings of the present study are that (i) trail runners have a greater maximal power than their road runners counterparts; (ii) the higher power was caused by a more force-oriented force-velocity profile, i.e. higher F_0 , despite no differences in isometric strength; (iii) road runners have a lower Cr than trail runners during level treadmill running at 14 km/h, while there are no Cr differences when running uphill, (iv) none of the biomechanical variables assessed were different between road and trail runners.

Force-velocity profile and isometric strength

TRAIL were able to produce a significantly higher absolute maximal power in the cycle sprint test and they tended to produce a higher maximal relative power compared to ROAD. This higher maximal power was mainly produced because TRAIL showed a significantly higher F_0 , with no significant differences in v_0 . To our knowledge, only another study has examined force-velocity profile characteristics of male runners, examining recreational marathon runners (Nikolaidis & Knechtle, 2020). Compared to the present study, they found higher F_0 and P_{\max} for the runners between 20 and 35 years of age, with similar relative P_{\max} . Interestingly, our results show lower maximal power than what has been reported in the literature for track sprinters and middle-distance runners (1168 ± 103 and 1020 ± 90 W respectively) (Granier et al., 1995). In the present study, no differences were found in isometric strength, relative to body mass, of the KE and KF muscles. It is worth mentioning that knee extensor strength was found to be correlated with trail running performance in other studies (Balducci, Cléménçon, et al., 2017; Ehrström et al., 2018). The higher force and power production by trail runners could be attributed to the greater amount of steep uphill and downhill training that trail runners perform compared to road runners,

even though TRAIL performed less resistance training than ROAD. Conversely, it is well known that there is an interference effect when combining endurance and resistance training, decreasing the magnitude of the strength adaptations (Coffey & Hawley, 2017). As ROAD did more endurance training than TRAIL, it is possible that their endurance training interfered with the adaptations from the strength training, offsetting their higher strength training volume. The lack of significant differences in v_0 could be due to the fact that running speeds and step frequency are so far from the movement velocity at v_0 that v_0 may not reflect any differences between trail and road runners.

Cost of running and biomechanical measures

As it was hypothesised, Cr_{FLAT} was lower for ROAD compared to TRAIL, significantly at 14 km/h and there was a trend at 10 km/h. Contrary to our hypothesis, there were no significant differences between groups in Cr_{UH} . This could possibly be explained by the incline of the treadmill not being steep enough. In other words, it is possible that measuring Cr at steeper inclines ($\geq 15\%$) would show greater differences in Cr between the two groups, since those are inclines more specific to trail running. We did not test Cr_{UH} at steeper inclines due to the limitations of our equipment.

No differences between TRAIL and ROAD were found in flight time, contact time, step frequency, duty factor, leg stiffness or vertical stiffness in any of the measured conditions. This was despite ROAD training and competing at faster speed, which leads to shorter contact times. It could have been expected that former track runners (6 of the 7 ROAD athletes) would have a more dynamic running pattern, with shorter contact times, due to their higher training and racing speeds and the track surface.

Training and racing

Several studies have investigated the training of elite road runners, reporting that elite road runners run an average of 182 to 206 km/week during marathon preparation (Billat et al., 2001; Enoksen et al., 2011) but studies describing the typical training of elite trail runners have not been published yet. Interestingly, TRAIL reported only 55% of the monthly training hours reported by ROAD, with ROAD training more hours than TRAIL in every type of training and TRAIL performing only 38% of the monthly resistance training hours reported by ROAD. These findings

were not totally expected for two main reasons. First, trail runners compete in events of longer duration than road runners, which may require higher training volumes. Second, our sample included national-level road runners, who are not all international elite (i.e. their best 10,000 m time was 6.9% to 17.7% slower than the current world record) while the group of trail runners in our study were elite international athletes, including all athletes on the winning team in the Trail World Championships and the fourth place on the World Mountain Running Championships the season they were tested. It has been previously suggested (Millet, 2012) that elite athletes in trail running are not comparable with elite road runners because, even if they win international competitions, their performance level is lower due to trail running being a younger sport with less incentives in the form of prize money. Our data adds evidence to this idea, however, further research on the physiological determinants of performance in endurance sports, such as maximal oxygen consumption, should be done to compare elite trail runners with other elite endurance athletes.

In terms of racing, there were no significant differences between the number of races per year between ROAD and TRAIL. However, the average duration of the races completed by TRAIL was longer (2:22 h, range 0:02:42 to 14:19 h) than the duration of races completed by ROAD (0:44 h, range 0:01:59 to 2:20 h). This meant that the total duration spent competing was, on average, 30:21 h for TRAIL, and only 12:36 h for ROAD. Our study also shows that elite runners specialize and compete mainly in one discipline, with little crossover between trail and road racing.

Limitations

This was an observational study, and its design does not allow to find the cause of the differences that have been found between trail and road runners. It is possible that the individual physiological characteristics nudge athletes to compete in the specific discipline where they think they may be better, but it is also possible that the choice of discipline comes first, and the specific training creates specific adaptations. Therefore, it is not possible to discern if the differences that have been found are caused by nature or nurture.

Cost of running and running biomechanics testing was performed at relatively low speeds, of 10 and 14 km/h, while other studies have tested runners at faster speeds, commonly 16 km/h (Jones, 2006). Conversely, uphill running was tested at only 10% incline. This was due to the

equipment limitations, because the treadmill used needed to be transported to training camps, and it was not able to achieve high speeds or inclines. It is possible that the low speeds might have been too low for ROAD, who may have been tested at suboptimal speeds, because they might be habituated to training and competing at higher speeds. However, the running intensities were low enough for all athletes to be in the moderate intensity domain, which made the comparison physiologically equivalent, even if they ran at different percentages of their competition speed or their velocity at $\dot{V}O_2\text{max}$. Similarly, a 10% incline may not have been steep enough to show differences between road and trail runners.

The fact that we aimed to test elite athletes (the 10 trail runners of the present study were all in the best 268 trail runners in the world) implies necessarily that the sample of athletes that can be measured is low. We tested all the elite athletes that were invited to the training camps organized by the French Athletics Federation.

As the athletes in this study were tested during training camps, preparing for racing objectives, the testing that could be done was limited, i.e. the athletes and coaches only accepted submaximal testing or testing of short duration. Therefore, there are many physiological variables that could not be measured, but that may be different between trail and road runners, such as $\dot{V}O_2\text{max}$, which is a well-known predictor of endurance performance. However, among elite athletes, $\dot{V}O_2\text{max}$ does not explain differences in performance (Pollock, 1977), so studying the differences in other characteristics, such as neuromuscular characteristics and Cr is important. The potential injury risk was the reason why force-velocity testing was completed using a cycle ergometer, instead of using loaded jumps or running sprints, which may have been more specific and shown greater differences, but may be associated with greater risk of injury, and the performance staff did not accept sprint running tests. Furthermore, trail runners were not used to performing loaded jumps or running sprints, while road runners had more experience in these types of exercise, which could give road runners a technical advantage. Measuring the FVP on a bicycle ergometer allowed us to look at the physiological while decreasing the effect of technical ability.

Conclusion

The findings from this study suggest that elite trail runners have a different neuromuscular profile from road runners, with trail runners being stronger and more powerful while road runners

have a lower cost of running during level (but not uphill) running. However, it is not clear if those differences are caused by the differences in training for each specific discipline, either the type (e.g. denivelation) or the amount of training, since this study also shows that road runners train significantly more. Further research should focus on measuring other variables, such as differences in maximal aerobic and anaerobic capacity, as well as measuring Cr at higher speeds and steeper inclines.

Practical applications

No previous study has compared the differences between road and trail elite runners. Our results are of interest for athletes, coaches and practitioners working with trail runners as well as road runners, as they highlight some of the differences between elite road and trail runners, which can help design specific preparation strategies for each discipline. Trail runners should pay special attention to neuromuscular factors, i.e. developing strength and power. This may be especially relevant to road runners who wish to change disciplines to compete in trail running.

In terms of training, we show that there is a gap in the amount of time dedicated to training when comparing elite road and trail runners, with trail runners training much less, on average. This suggests that it takes less training to become a world class athlete in trail running compared to road running, i.e. that the ‘maturity’ of the two disciplines differs. Increasing training volume of trail runners may present an opportunity to increase their level of performance.

3.4. Performance determinants of trail running races of different distances (Study 2)

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Introduction

The physiological determinants of middle and long-distance running have been widely studied in the past. It is well known that endurance running performance is predicted by maximal oxygen uptake ($\dot{V}O_{2\max}$), running economy, and fractional utilisation of $\dot{V}O_{2\max}$, which is sometimes measured from the lactate or ventilatory thresholds (Joyner & Coyle, 2008; Midgley et al., 2007). The relative influence of each one of these parameters is believed to vary depending on the duration of the event. For instance, $\dot{V}O_{2\max}$ is a better predictor of performance at shorter distances (5 km), and fractional utilisation and running economy become more important as distances increase (marathon and 84.6 km) (C. T. M. Davies & Thompson, 1979; M. L. Pollock, 1977). Predictors of performance over ultra-marathon distances have rarely been addressed. It was found that $\dot{V}O_{2\max}$ and percentage of velocity at $\dot{V}O_{2\max}$ sustained were predictors of performance during a 24-h treadmill run (Millet et al., 2011). Furthermore, the percentage of velocity at $\dot{V}O_{2\max}$ sustained during the race was predicted by running economy (Millet et al., 2011). In trail running, no relationships have been found between any physiological variables and performance in races longer than 24 h (Coates et al., 2021; Gatterer et al., 2020).

Besides the abovementioned factors, performance is influenced by external factors such as race characteristics (terrain, elevation profile) and environmental conditions (weather, altitude). Identifying the physiological determinants of performance in trail running is challenging (de Waal et al., 2021) since trail running races can vary more than road running races in terms of duration, distance, elevation gain and the technical difficulty of the terrain (Scheer et al., 2020); as well as the environmental conditions, often including altitude and extreme weather. The physiological determinants of trail running performance have been less investigated than those of road running. Trail running performance is influenced by parameters such as $\dot{V}O_{2\max}$ (Balducci, Cléménçon, et

al., 2017; Ehrström et al., 2018; Gatterer et al., 2020), lactate and ventilatory thresholds (Scheer, Vieluf, et al., 2019) and running economy (Ehrström et al., 2018; Scheer, Janssen, et al., 2019). However, how those parameters contribute to performance has generated some debates in the literature. For example, there was no relationship between running economy and trail running performance in a 75 km race (Balducci, Cléménçon, et al., 2017). One possible reason is that running economy may not be as critical for running performance during long duration trail running events (Millet et al., 2012). It has been suggested that ultramarathon trail runners deliberately use strategies that decrease running economy but may protect from muscle damage and fatigue, improving the ability to run faster later in the race and therefore performance (Millet et al., 2012). Other factors beyond aerobic capacity have been shown to influence trail running performance. Measures of body composition such as body mass index (BMI) and adiposity (Alvero-Cruz et al., 2019) and muscle factors including maximal isometric strength and strength-endurance of the knee extensor (KE) muscles have been reported to influence trail running performance (Balducci, Cléménçon, et al., 2017; Ehrström et al., 2018).

The physiological predictors of performance in trail running vary between studies. A wide variety of trail running races exists, and performance predictors have been studied in races ranging from 27 to 160 km, which limits the generalization of the results. Knowing the factors that determine performance in trail running races of different distances could be useful to create specific training programs for different race distances or to select the race distances that best suit the strengths of each athlete. To date, only two studies have compared the performance determinants of trail running races of different distances in similar conditions, finding that aerobic capacity parameters were related to performance on a 68 km trail running race, but not a 121 km race (Gatterer et al., 2020) and that aerobic capacity was related to performance in 50 and 80 km trail races, but no variables explained performance over 160 km (Coates et al., 2021). Despite different running distances for the longest races in those studies, the elevation gain in the study by Coates et al. (2021) was lower, resulting in similar average finishing times of 25 h and 28 h. The purpose of our study was thus to determine the physiological factors that predict performance in trail running races of different distances, ranging from 40 km to 170 km and from a duration of 4 h 30 min to 45 h.

Methods

Overview

Seventy-five experienced recreational trail-runners who were participating in one of the races of the Ultra-Trail du Mont Blanc (UTMB®) in Chamonix, France, were recruited for this study, of which 54 completed their event and were thus included in the analysis. Runners participated in one of five races described in Table 6 and happening during the same week. Weather was similar for all races, with temperatures at the finish line ranging from 11°C to 31°C and no precipitation (*Past Weather in Chamonix Mont-Blanc, Haute-Savoie, France — August 2019*, 2019). Participants visited the laboratory four to eight weeks before the race. They provided informed consent and were examined by a medical doctor. Subsequently, participants performed baseline testing including anthropometry and a treadmill test. Participants were familiarised with the testing procedures that would happen before and after the races. Participants visited the laboratory two more times, 24-48 h before the race and immediately afterwards, to assess maximum voluntary contraction (MVC), power-force-velocity-profile (FVP), neuromuscular fatigue, and running economy.

The study obtained ethical approval from the French Ethical Research Committee (Comité de Protection des Personnes Ouest VI) and was conducted in accordance with the Declaration of Helsinki (2013). It was part of a larger study on the effects of trail running distance on fatigue, registered at ClinicalTrials.gov (NCT04025138).

Anthropometry

Participant's height, weight and body fat percentage (Durnin & Womersley, 1974) (BF) were measured during the first visit. Weight was measured again during the second visit to the laboratory, and immediately after the end of the race.

Table 6. Race characteristics of the UTMB trail races.

Race Characteristics	SHORT		MEDIUM	LONG	
	MCC	OCC	CCC	TDS	UTMB
Distance (km)	40	55	101	145	170
D+ (m)	2300	3500	6100	9100	10000
ITRA KM-effort	63	90	162	236	270
ITRA Category	S	M	XL	XXL	XXL
Maximal Temperature at the Finish Line (°C)	30	30	31	30	31
Male Winning Time (hh:mm:ss)	3:40:46	5:19:24	10:28:49	18:03:06	20:19:07

D+, total elevation gain; ITRA, International Trail Running Association.

Treadmill tests

An incremental treadmill (EF 1800, HF Tecmachine, Andrézieux-Bouthéon, France) test was performed during the first visit, with gas exchange measurements (Metamax 3B, Cortex GmbH., Leipzig, Germany). The test started with a 4-minute level run at 10 km/h, which was used to measure cost of running (Cr). Cr was calculated from the values of oxygen uptake, carbon dioxide production and respiratory exchange ratio during the last minute of the running bout, after checking that a steady state had been achieved (Péronnet & Massicotte, 1991). The percentages of energy coming from lipids (%Fat10) and carbohydrates (CHO) as well as the total CHO oxidation rate were also calculated. After a 1-minute rest period, an incremental running test at 12% incline was performed as described by Sabater Pastor et al. (2021). The highest 30-second $\dot{V}O_2$ value was taken as $\dot{V}O_{2max}$ and the average velocity during the last minute v_{Peak} was recorded. Ventilatory thresholds (gas exchange threshold, GET; and respiratory compensation point, RCP) were determined according to Wasserman et al. (1994) The speed and $\dot{V}O_2$ associated with GET and RCP were determined.

During visits 2 and 3, Cr was measured, to assess changes in running economy associated with fatigue, as explained by Sabater Pastor et al. (2021).

Power-Force-Velocity Profile and Maximal Isometric Force

The FVP was measured using two 7-s sprints on a cycle ergometer, as explained by Koral et al. (2021). Both sprints were combined on a FVP (Krüger et al., 2020) to obtain the parameters: F_0 (theoretical maximal force), v_0 (theoretical maximal velocity) and P_{\max} (the apex of power-velocity parabolic relationship), which was calculated as $F_0 \times v_0 / 4$ (Morin & Samozino, 2016). All parameters are presented relative to body mass.

The MVC of the KE and plantar flexors (PF) were assessed during visit 2 and visit 3 as reported previously (Besson et al., 2021). The highest MVC value obtained for both, KE and PF, was normalized to body mass to obtain the relative MVC.

Neuromuscular fatigue

Neuromuscular fatigue was quantified for KE MVC, PF MVC and P_{\max} as the percentage difference from the pre-race measurement.

Data Analysis

Relative race performance ($PERF_{\text{rel}}$) was calculated relative to the absolute (male) winning time of the respective race and corrected for performance level of the winner, using the international running association performance index (<https://itra.run/content/indice-performance>), which is calculated linearly from a maximum of 1000, where 1000 is a theoretical best possible performance in that race. The score obtained by the runner is thus its relative performance compared to the theoretical best. Therefore, $PERF_{\text{rel}}$ was calculated using the equation:

$$PERF_{\text{rel}} = ((\text{subject time} / \text{winning time}) / (\text{winner's PERF index}) / 1000)$$

The correction for performance level of the winner was calculated because the winners of the different races have similar, but not equivalent, performance levels ranging from 860 to 928 points.

The races were grouped in three groups for the statistical analysis: SHORT (MCC and OCC, < 60 km), MEDIUM (CCC, 101 km) and LONG (TDS and UTMB, >140 km) (Table 6).

Statistical Analysis

Data are presented as mean \pm SD in the text, tables and figures. Normal distribution was assessed using the Shapiro-Wilk test. Differences between races were assessed using one-way ANOVA with Tuckey post-hoc tests in case of significant main effect. The correlation of each of the measured variables with $PERF_{rel}$ was assessed using correlation matrix analysis and Pearson's product moment correlation coefficient (r) or Spearman rank-order correlation (ρ) if the assumption of normality was not respected. Stepwise multivariate linear regression analysis was performed to determine the variables that best explained $PERF_{rel}$. After controlling for multicollinearity, only the most physiologically sound variables were selected and inserted in the model. Significance was set at $P < 0.05$. Statistical analysis was performed using jamovi (version 1.2.27, the jamovi project).

Results

Performance and Baseline Characteristics

Finishing times for the races are presented in Figure 19A. Finishing time of SHORT was significantly lower than MEDIUM and LONG ($p < 0.001$), and time of MEDIUM was significantly lower than LONG ($p < 0.001$). There was no significant effect of race distance on $PERF_{rel}$ ($p = 0.090$), with average $PERF_{rel}$ being similar for all races (Figure 19B). There was no overlap in race duration between SHORT and MEDIUM, and only the fastest runner of LONG completed their race in less time than the slowest runners of MEDIUM. Baseline characteristics of the participants are presented in Table 7.

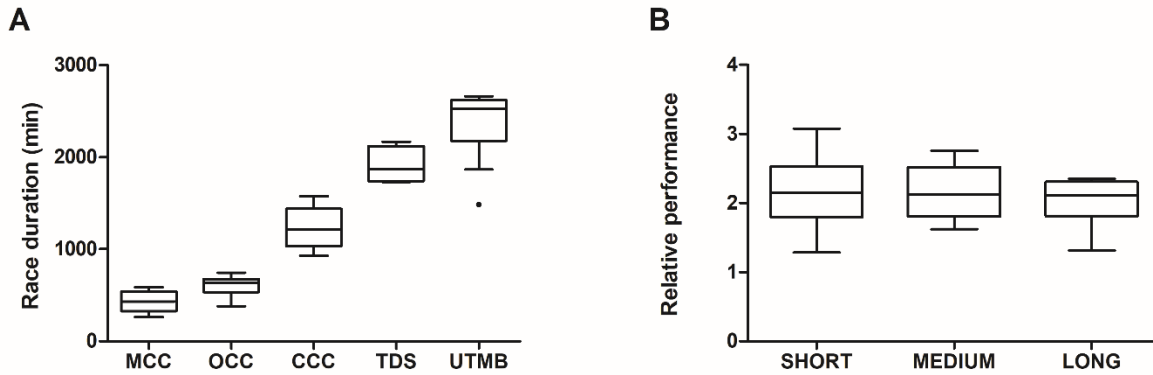


Figure 19. Finishing times (panel A) and relative performance (panel B) of finishers of the UTMB races. Dot under UTMB box plot in panel A is an outlier as defined by Tukey: value lower than 25th percentile minus 1.5 times the interquartile range.

Treadmill Test and Performance

The different measures of aerobic fitness obtained from the treadmill test (i.e., $\dot{V}O_2\text{max}$, $v\text{Peak}$, $\dot{V}O_2$ and speed at the ventilatory thresholds) were highly correlated to each other (Pearson's r range from 0.835 to 0.949, $p < 0.001$ for all correlations), therefore only the variables that showed the highest correlation coefficients with performance are presented (Figure 20). Performance in SHORT was related to $\dot{V}O_2\text{max}$ ($r = -0.856$, $p < 0.001$) and $v\text{Peak}$ ($r = -0.847$, $p < 0.001$), as well as %Fat10 ($r = -0.593$, $p = 0.006$) and CHO oxidation rate ($r = 0.65$, $p = 0.002$) at 10 km/h. The correlation between performance in SHORT and Cr at 10 km/h did not reach significance ($r = 0.432$, $p = 0.057$). Performance in MEDIUM was related to $\dot{V}O_2\text{max}$ ($r = -0.924$, $p < 0.001$) and $v\text{Peak}$ ($r = -0.898$, $p < 0.001$), but not to Cr or substrate utilisation. Performance in LONG was significantly correlated with $v\text{Peak}$ only ($r = -0.617$, $p = 0.019$). There was no correlation between GET and RCP expressed relative to $\dot{V}O_2\text{max}$ or $v\text{Peak}$ and performance.

Table 7. Baseline characteristics of finishers.

	SHORT		MEDIUM		LONG	
	Females	Males	Females	Males	Females	Males
Number of Participants	11	13	4	12	6	8
Age (years)	36.3 ± 10.2	34.8 ± 7.6	34.3 ± 6.3	37.2 ± 10.4	39.2 ± 6.7	41.6 ± 8.9
Weight (kg)	60.4 ± 5.1	74.9 ± 12.7	59.1 ± 23.7	74.6 ± 14.1	54.5 ± 7.1	72.7 ± 11.0
Height (cm)	167.3 ± 6.4	178.1 ± 7.1	164.0 ± 3.6	179.6 ± 3.5	162.6 ± 7.9	178.1 ± 5.1
BMI (kg/m ²)	21.2 ± 1.1	23.2 ± 3.6	22.0 ± 1.9	23.1 ± 2.1	20.6 ± 1.3	23.0 ± 2.8
Body Fat Percentage (%)	25 ± 6.6	17.7 ± 6.3	23.7 ± 6.1	14.1 ± 5.2	23.8 ± 5.0	12.8 ± 4.3
Aerobic Capacity						
$\dot{V}O_2$ max (ml/kg/min)	53.5 ± 4.6	61.7 ± 11.2	54.9 ± 5.1	61.7 ± 6.6	53.7 ± 5.0	62.4 ± 5.7
vPeak (km/h)	9.3 ± 0.9	10.8 ± 1.6	9.2 ± 0.6	11.2 ± 1.2	9.3 ± 1.0	11.2 ± 1.0
Cr (J/kg/m)	4.5 ± 0.2	4.5 ± 0.4	4.9 ± 0.2	4.4 ± 0.3	4.5 ± 0.2	4.7 ± 0.6
Neuromuscular Function						
KE MVC (N·m/kg)	3.2 ± 0.5	3.8 ± 0.7	2.9 ± 0.8	4.1 ± 0.9	3.2 ± 0.7	3.9 ± 0.8
PF MVC (N·m/kg)	1.9 ± 0.5	2.2 ± 0.4	2.1 ± 0.4	2.4 ± 0.3	2.1 ± 0.6	2.2 ± 0.3
P _{max} (W/kg)	8.6 ± 0.9	10.5 ± 1.6	9.2 ± 0.6	11.8 ± 1.9	8.1 ± 1.3	10.2 ± 1.1

BMI, body mass index; vPeak, average speed of the last minute of the incremental test; Cr, cost of running; KE, knee extensors; MVC, maximal voluntary contraction; PF, plantar flexors; P_{max}, maximal power during the 7-s sprints.

Anthropometry and Performance

Unlike LONG, performances in SHORT and MEDIUM were significantly related to BF ($r = 0.749$, $p < 0.001$ and $r = 0.830$, $p < 0.001$, respectively). There was no relationship between performance in any distance and BMI, body mass, or total fat free mass. BF was also correlated with $\dot{V}O_2$ max ($r = -0.782$, $p < 0.001$).

Power-Force-Velocity Profile, Maximal Isometric Force and Neuromuscular Fatigue

There were significant relationships between performance in SHORT and KE MVC ($r = -0.567$, $p = 0.005$), PF MVC loss after the race ($r = -0.455$, $p = 0.033$), F_0 ($r = -0.574$, $p = 0.003$), and P_{\max} ($r = -0.422$, $p = 0.040$). Performance in MEDIUM was significantly correlated to P_{\max} ($r = -0.690$, $p = 0.006$), F_0 ($r = -0.636$, $p = 0.015$) and KE MVC ($r = -0.545$, $p = 0.036$). Performance in LONG was not related to any neuromuscular variables.

Regression Models

Full regression models are shown in Table 8. After controlling for multicollinearity, the independent variables selected to be introduced in the model were BF, $\dot{V}O_{2\max}$, GET and RCP expressed as percentage of $\dot{V}O_{2\max}$, Cr, %Fat10, KE MVC and P_{\max} obtained from the FVP. The regression model for LONG could not be performed, since the distribution of the dependent variable, $PERF_{\text{rel}}$, was not normal.

Table 8. Multivariate models predicting trail running performance in SHORT and MEDIUM races.

Race	Variable	Coefficient (SE)	Standardised Coefficient	P value	R ² (Adjusted R ²)	Model P Value
SHORT	$\dot{V}O_{2\max}$	-0.034 (0.005)	-0.759	< 0.001	0.825 (0.790)	< 0.001
	%Fat10	-0.007 (0.003)	-0.267	0.045		
MEDIUM	$\dot{V}O_{2\max}$	-0.066 (0.007)	-0.972	< 0.001	0.917 (0.893)	< 0.001
	KE MVC	0.466 (0.078)	0.551	< 0.013		
	Body Fat %	0.022 (0.008)	0.445	0.072		

$\dot{V}O_{2\max}$, maximal oxygen uptake; %Fat10, percentage of energy derived from lipids at 10 km/h; KE MVC, knee extensor maximal voluntary contraction; Body Fat %, body fat percentage.

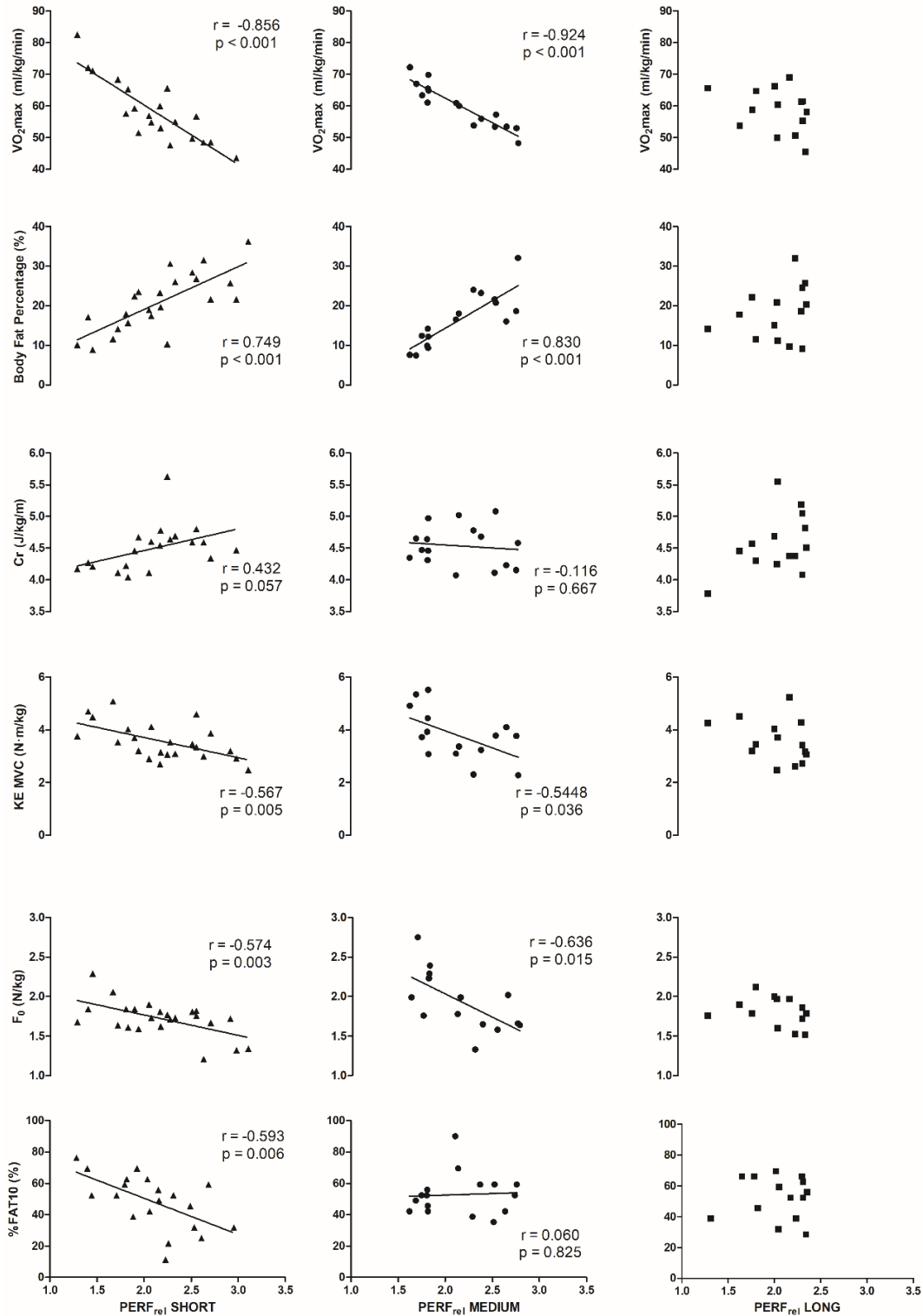


Figure 20. Correlations between physiological variables and relative performance. $\dot{V}O_2\text{max}$, maximal oxygen uptake; Cr, cost of running; KE, knee extensor; MVC, maximal voluntary contraction; F_0 , theoretical maximal force in the power-force-velocity profile; %FAT10,

percentage of total energy consumed derived from fat while running at 10 km/h; PERFrel, performance relative to the time of the male winner, adjusted for his ITRA performance index.

Discussion

The aim of this study was to determine which physiological variables can explain trail running performance in races of different distances. It was found that performance in SHORT (40 to 55 km, 2300 to 3500 m D+) was predicted by $\dot{V}O_{2max}$ and %Fat10. Performance in MEDIUM (100 km, 6100 m D+) was predicted by $\dot{V}O_{2max}$, isometric KE MVC, and adiposity. Performance in LONG was only associated to vPeak but since performance was not normally distributed for this distance, a linear model should not be fitted to the data. Overall, these data suggest that (i) $\dot{V}O_{2max}$ becomes a less important contributor as distance increases likely because other factors such a resistance to muscle damage play a significant role, (ii) unlike what is sometimes stated, a high capacity to oxidize fat and a lower percentage body fat are more important for short/medium than for long distances and (iii) isometric and dynamic force are also important in shorter distances. These results have clear implications on training and nutrition strategies of trail runners.

Metabolic Power during the Races

Several variables related to aerobic capacity were measured during the first session, including $\dot{V}O_{2max}$ and vPeak, as well as $\dot{V}O_2$ and speed at GET and RCP. All of these variables correlated with performance in SHORT and MEDIUM, with $\dot{V}O_{2max}$ showing the greatest correlation. It is well known that maximal aerobic capacity is the main predictor of long-distance running performance in road running, but the importance of $\dot{V}O_{2max}$ seems to decrease as distance increases (C. T. M. Davies & Thompson, 1979). Performance in trail running has been associated with $\dot{V}O_{2max}$ and/or vPeak in races of 27 to 107 km (Alvero-Cruz et al., 2019; Ehrström et al., 2018; Fornasiero et al., 2018; Lazzer et al., 2012; Martinez-Navarro et al., 2020). The correlation coefficients between $\dot{V}O_{2max}$ or vPeak and performance were higher in the present study compared to the literature, ranging from -0.61 to -0.85 for the cited studies, while we found higher correlation coefficients of -0.86 and -0.92 for $\dot{V}O_{2max}$ for SHORT and MEDIUM. In the regression models, $\dot{V}O_{2max}$ was the best predictor of performance for both, SHORT and MEDIUM, explaining by itself 75.6% and 83.1% of the variability in performance. Other studies have shown $\dot{V}O_{2max}$ to be an important predictor in regression models of trail running

performance (Alvero-Cruz et al., 2019; Balducci, Cl  men  on, et al., 2017; Ehrstr  m et al., 2018; Fornasiero et al., 2018; Martinez-Navarro et al., 2020; Scheer, Janssen, et al., 2019).

Performance in LONG correlated only with vPeak, despite a strong correlation between vPeak and $\dot{V}O_2\text{max}$ ($r = 0.871$, $p < 0.001$). $\dot{V}O_2\text{max}$ and not vPeak was used as a performance predictor in our regression models, due to the high correlation between them, because $\dot{V}O_2\text{max}$ is more stable and less test-dependent than vPeak, (Iannetta, Azevedo, et al., 2019) and therefore would make future comparisons across the literature more difficult. Only two other studies (Coates et al., 2021; Gatterer et al., 2020) have assessed the relationship between performance and $\dot{V}O_2\text{max}$ or vPeak in trail running races longer than 24 h (121 and 160 km). $\dot{V}O_2\text{max}$ was the main predictor of performance in a flat, 24h treadmill test (Millet et al., 2011). No relationship was found between performance and $\dot{V}O_2\text{max}$, or any other variable in either of the trail running studies. However, the samples were only seven (Gatterer et al., 2020) and eight runners (Coates et al., 2021) so more studies including bigger sample sizes should be done to ascertain if there is a relationship between performance in long trail running races and maximal aerobic capacity. Of note, unpublished data from our laboratory from the UTMB in 2009 (Millet et al., 2011) (166 km, 9500 m D+) shows a strong negative correlation between race time and $\dot{V}O_2\text{max}$ ($r = -0.724$, $p < 0.001$, $N = 22$, Figure 33, Chapter 5).

Several other studies have assessed the influence of threshold variables on trail running performance. Similarly to our results, some studies found a relationship between speed or $\dot{V}O_2$ at first and second threshold and trail running performance (Fornasiero et al., 2018; Martinez-Navarro et al., 2020; Scheer, Janssen, et al., 2019; Scheer, Vieluf, et al., 2019). The correlations between speed and $\dot{V}O_2$ at GET and RCP were expected considering the strong correlations between the threshold variables and vPeak and $\dot{V}O_2\text{max}$. Importantly, there were no significant correlations between thresholds expressed relative to vPeak or $\dot{V}O_2\text{max}$ and performance. Possible reasons why $\dot{V}O_2\text{max}$ and threshold measures are not associated with performance in races longer than 24 h include the fact that resistance to muscle damage or gastrointestinal distress may contribute more to the impairment of performance in long than in short races (Millet et al., 2012), therefore decreasing the importance of aerobic capacity. In addition, total time is less influenced by running speed than in shorter races, since participants take breaks or even deciding to take nap on the course.

PERF_{rel} in SHORT correlated positively with CHO oxidation rate and negatively with percentage of energy derived from lipids at 10 km/h, while there was no correlation between PERF_{rel} and substrate utilisation in other distances. However, percentage of energy derived from lipids was included as a significant predictor in the regression models of SHORT PERF_{rel}. The importance of fat oxidation is probably related to the sparing of glycogen during the races. Glycogen depletion is known to negatively affect performance in endurance exercise contributing to excitation-contraction coupling failure (Ørtenblad et al., 2011). The fact that lipid utilization is related to performance in SHORT but not longer races may seem paradoxical, but it may be related to the ability to ingest nutrients during the race and lower intensity. It is likely that (i) the lower energy expenditure in the LONG races makes the limited CHO intake a higher percent of total expenditure and (ii) the lower intensity allows for greater ingestion of CHO, both factors contributing to glycogen sparing and decreasing the importance of endogenous fat utilisation. To the best of our knowledge, only one other study has assessed the relationship between substrate oxidation and trail running performance (Martinez-Navarro et al., 2020), finding a correlation between performance in a 107 km race and maximal fat oxidation rate in both men and women.

Cost of Running and Anthropometry

Cr has been considered a better predictor of long-distance road running performance than $\dot{V}O_2$ max in homogenous groups in terms of performance (Conley & Krahenbul, 1980). In the present study, there was no significant correlation between Cr and PERF_{rel} in any distance. No relationship was found between Cr and performance in a 75 km race (Balducci, Cl  men  on, et al., 2017) or 50 to 160 km races (Coates et al., 2021), while Cr was either a correlate or a predictor of performance in shorter races such as a 27 km trail race (Ehrstr  m et al., 2018), or a 3 stage 90 km race (30 km per day) (Lazzer et al., 2012). Overall, Cr seems more related to performance in shorter distances. The technicality of the terrain during trail running may be another reason why Cr is not related to performance. Indeed, a comparison of track runners and orienteers running in a flat path and in rough terrain showed that, despite no differences in Cr on the flat, the Cr of track runners increased significantly more than the Cr of orienteers when running in rough terrain, suggesting that the better technical ability of orienteers contributed to minimising the increase in Cr caused by the terrain (Jensen et al., 1999). The relationship between Cr measured on technical terrain and trail running performance still has to be assessed.

Performance in SHORT and MEDIUM correlated significantly with BF, but no other anthropometric variables correlated with performance. BF was included as a predictor only in the MEDIUM regression model. There was no relationship between anthropometric variables and LONG $PERF_{rel}$, possibly due to the distribution of performances, or to greater mass being less detrimental to performance at lower intensity (Millet et al., 2012). Other studies found low BF to be a significant predictor of trail running performance (Alvero-Cruz et al., 2019; Fornasiero et al., 2018), in races of 27 and 65 km; and a correlate of performance in a 107 km race (Martinez-Navarro et al., 2020). Low percentages of body fat are probably beneficial in trail running, since runners must carry their own body mass against the force of gravity during uphill, and slow it down during downhill, increasing the eccentric force demands (and muscle damage) of each step. Moreover, body fat affects aerobic capacity negatively, since $\dot{V}O_{2max}$ is expressed relative to body mass, and there was a significant negative relationship between $\dot{V}O_{2max}$ and BF in our sample of trail runners. This high correlation between $\dot{V}O_{2max}$ and BF may be the reason why BF was not included in the SHORT regression model.

Neuromuscular function at rest and with fatigue

One originality of the present study is the examination of neuromuscular variables that have rarely been considered. Performance in SHORT and MEDIUM was significantly related to neuromuscular performance in isometric KE as well as F_0 and P_{max} , while there was no relationship between neuromuscular function and performance in LONG. Furthermore, KE MVC was a predictor of $PERF_{rel}$ in the regression model of MEDIUM. Interestingly, while there was a negative correlation between KE MVC and $PERF_{rel}$ in SHORT and MEDIUM, showing that greater strength correlates with better performance, the estimate of KE MVC in the regression model was positive, meaning that greater relative KE MVC was associated with worse performance, after controlling for $\dot{V}O_{2max}$ and BF. This might be related to muscle fiber type as participants with higher content of fast-twitch fibers in their knee extensors might be able to produce more force, and those fast-twitch fibers may be detrimental for ultra-endurance running performance, since they are more prone to fatigue than slow-twitch fibers (Bottinelli & Reggiani, 2000). In the literature, a significant correlation was reported between higher KE MVC and better performance in a 75 km race (Balducci, Cl  men  on, et al., 2017), and no relationship was found between performance and concentric or eccentric KE MVC (Ehrstr  m et al., 2018).

In the present study, the only relationship between fatigue and performance was found for SHORT, where better performance was related to greater loss in PF MVC. It is possible that the ability to reach deeper levels of fatigue may be an advantage in endurance running events (Millet, 2011), particularly in short-distance races because of the higher intensity and partly because ultramarathon runners are known to use more strategies that may decrease fatigue of the leg muscles (Millet et al., 2012), such as using hiking poles. In fact, only 67% of the SHORT athletes used poles during their race, while 94% of the athletes in MEDIUM and LONG used them.

Limitations

The main limitation of our study is the relatively small sample size, which was affected by the high dropout rate during the races. Only 54 of the 75 trail runners included in the study were able to complete the races and were therefore included in the analysis. This was not explained by physiological differences between finishers and non-finishers. The low sample size may also be the cause of the lack of normally distributed data in LONG. Another limitation is that Cr was measured on treadmill rather than on trail. Finally, other non-physiological variables potentially impacting performance during trail running (e.g. technical ability, ability to ingest food, mental skills, etc) were not measured in this study.

Practical applications

The results of the present study suggest that aerobic fitness, specifically $\dot{V}O_2\text{max}$, is an important determinant of performance in trail running races up to 100 km and 20 h of duration, its importance decreasing in ultra-distances.. This suggests training methods aiming to enhance $\dot{V}O_2\text{max}$ must be considered for runners preparing ultra-trail races up to at least 100 km. Further, it was found that leg strength and power are also associated with performance in races shorter than 100 km. This information could help coaches and athletes, guiding them to better design of training plans to prepare for this type of events, in particular emphasizing the role of resistance training.

Conclusion

Maximal aerobic capacity was determinant for distances up to 100 km but the present study does not allow to completely rule out its importance for longer distances. Performance in shorter races (~50 km) was also predicted by lipid utilisation at slow speed, while other predictors of performance for the 100 km distance were maximal strength and body fat percentage. Future

studies should measure Cr over the specific gradient and terrain (i.e. on trail) as opposed to on a treadmill to better assess whether or not this is a predictor of trail running performance.

Résumé du Chapitre 3

- L'intensité qui peut être soutenue par les coureurs diminue à mesure que la durée augmente. Comme les courses de trail running sont plus longues que les courses sur route, il est courant que les épreuves de trail running soient courues à une intensité plus faible.
- Trois facteurs principaux influencent les performances en course de durée prolongée : la $\dot{V}O_2\text{max}$, la fraction de $\dot{V}O_2\text{max}$ qui peut être maintenue, qui est en corrélation avec les seuils métaboliques, et l'économie de course.
- Plusieurs études ont montré que la performance en trail running était corrélée à la $\dot{V}O_2\text{max}$ et aux seuils. La relation entre RE et la performance en trail running est moins claire.
- RE peut être mesurée comme le coût en oxygène ou le coût énergétique de la course. RE est affectée par plusieurs facteurs, notamment anthropométriques, biomécaniques et physiologiques, ainsi que par la pente à laquelle elle est mesurée.
- Dans l'étude 1, nous avons comparé des coureurs d'élite sur route et de trail. Nous avons montré que les coureurs de trail étaient plus puissants que les coureurs sur route lorsqu'ils étaient mesurés dans des conditions dynamiques, mais qu'ils étaient moins économes lorsqu'ils couraient à 14 km/h. Leur économie n'était pas différente des coureurs sur route lorsqu'ils couraient en montée à une pente de 10%. En outre, les coureurs de trail élite s'entraînaient moins que les coureurs sur route élite.
- L'étude 2 a montré que la performance dans les courses de trail de 40-60 km est déterminée par la $\dot{V}O_2\text{max}$ et l'oxydation des lipides, tandis que la performance dans les courses de 100 km est déterminée par la $\dot{V}O_2\text{max}$, la force maximale et le pourcentage de masse grasse. Les déterminants de la performance dans les courses de plus de 140 km ne sont pas encore clairs, mais le fait que la $\dot{V}O_2\text{max}$ puisse être liée à la performance sur ces distances ne peut être exclu.

4. Consequences of prolonged running on running economy

The mentioned factors in the previous sections influence performance during trail-running races. However, it is not known how these factors are modified after prolonged running, and it has been suggested that (i) prolonged endurance exercise may have a negative impact on these factors (Maunder et al., 2021), and (ii) faster marathon runners may be able to run races at higher speed relative to their critical speed due to lower deterioration of their critical speed after prolonged exercise (Jones et al., 2021). Even at relatively low intensities, in the heavy and even the moderate intensity domains, physiological changes with negative performance consequences occur over time. Despite the ability to achieve a steady state in $\dot{V}O_2$, blood lactate concentration or H^+ and inorganic phosphate, prolonged exercise induces increases in core and muscle temperatures (Febbraio et al., 1994), depletion of endogenous fuel sources such as glycogen (Ørtenblad et al., 2013; Watt et al., 2002), dehydration (Baker & Jeukendrup, 2014; Goulet et al., 2012; Goulet et al., 2013), and increases in circulating catecholamines (Zouhal et al., 2008), as well as muscle damage and failures in excitation-contraction coupling (Giandolini et al., 2016b; Lepers et al., 2002). These physiological changes could negatively affect the physiological determinants of performance, and therefore lead to performance impairment, seen as a reduction in the intensity of exercise. Indeed, it has been shown that critical power declines following exercise in the heavy domain at a constant load (Clark et al., 2018; Clark, Vanhatalo, Thompson, Wylie, et al., 2019), and this decline seems to be influenced by muscle glycogen depletion and CHO ingestion (Clark, Vanhatalo, Thompson, Joseph, et al., 2019; Clark, Vanhatalo, Thompson, Wylie, et al., 2019).

3.5. Changes in running economy after prolonged running exercise

Perhaps the physiological performance predictor that has received most attention regarding its deterioration after endurance exercise is the cost of locomotion (C_L). Several studies have shown an increase in C_L after prolonged cycling exercise ranging from as little as 20 min at 65% of $\dot{V}O_{2max}$ to two hours at 60% of maximal aerobic power (Hagan et al., 1992; Hagberg et al., 1978; Hopker et al., 2017; Passfield & Doust, 2000). In running, deterioration of Cr after running have been reported after high intensity efforts of 3 km (Candau et al., 1998), 60 min bouts at the maximal sustainable intensity (Hunter & Smith, 2007), after marathon running (Brueckner et al., 1991; H. Kyrolainen et al., 2000). Increases of Cr after ultra-distance treadmill running have also been reported, with Cr increasing after 8 h during a 24 h treadmill test (Gimenez et al., 2013), and

O₂C increased significantly by 18% after 5 hours of treadmill running at 55% of maximal aerobic velocity (Place et al., 2004). It also seems that higher intensities for a given duration, or greater durations for a given intensity, lead to greater deterioration of Cr. Xu and Montgomery (1995) found 2.5-4% greater increases in Cr after a 90 min run at 80% of $\dot{V}O_{2\max}$ than at 65% intensity, and Gimenez et al. (2013) reported greater deterioration in Cr for the subjects who sustained a higher intensity relative to $\dot{V}O_{2\max}$. Regarding duration, Brueckner et al. (1991) found that O₂C did not change after 15 km, but increased by 4.4% to 7.0% after 32 and 42 km during simulated marathon trials. This suggests that greater effort or greater fatigue induced by either higher intensities or longer durations may contribute to the increase in Cr during running. For instance, no changes in Cr were found during low-intensity efforts at intensities that could be sustained for a much longer duration such as at 15 km during a marathon (1991). Schena et al found that, despite a 7% increase in O₂C, Cr did not change significantly after a 60 km test at best 100 km pace in experienced ultramarathoners (Schena et al., 2014), and Gimenez et al. (2013) found that Cr did not change during the first 6 h of a 24-h treadmill running test, despite a significant increase in O₂C. This evidence suggests that there may be a minimum threshold of a combination of duration and intensity of exercise that is needed to produce an increase in Cr.

Several studies have measured changes in running economy following ultramarathon competitions, including trail running races. Interestingly, it has been suggested that running economy may improve after ultramarathon running. Vernillo et al. (2017) reviewed the published papers that have reported changes in running economy, measured either as O₂C or Cr. As can be seen in Figure 21, they found contradictory results, with some studies finding no effect of trail running on running economy, while others found an improvement and others a worsening of running economy. Lazzer et al. (2015) measured a significant 8.7% increase in O₂C while running at a self-selected pace after an uphill 43 km race with 3,060 m of climbing. However, it is important to note that the measurements were taken at sea level at the start line and immediately post-race near the finish line at 3,063 m above sea level. The difference in altitude and the hypoxia may have affected O₂C, independently of the race. In contrast, Millet et al. (2000) and Balducci et al. (2017) reported no significant changes in O₂C after mountain ultramarathon (65 km, 2500 m D+ and 75 km, 3920 D+, respectively). Lazzer et al. (2012, 2014) and Fusi et al. (2008) studied changes in O₂C after trail running stage races, including 90 km in three stages and 120 km in 5 stages. Only Lazzer et al. (2012) found a significant increase in O₂C after the third stage compared to baseline.

Lazzer et al. (2014) did find a significant effect of time (pre- to post-stage), but since there was no time \times stage interaction, the effect of post-race compared to pre-race could not be considered significant. Finally, Fusi et al. (2008) did not find any differences in O_2C yet they measured it “3-5 days after” the race most likely masking the acute running-induced effects on O_2C due to recovery. Interestingly, despite the significant increase in O_2C post-race found by Lazzer et al. (2012), they found a non-significant decrease in O_2C 5 days after the race (-9%, $p = 0.057$), showing that the changes in O_2C measured days after the race may not reflect the acute changes induced by running.

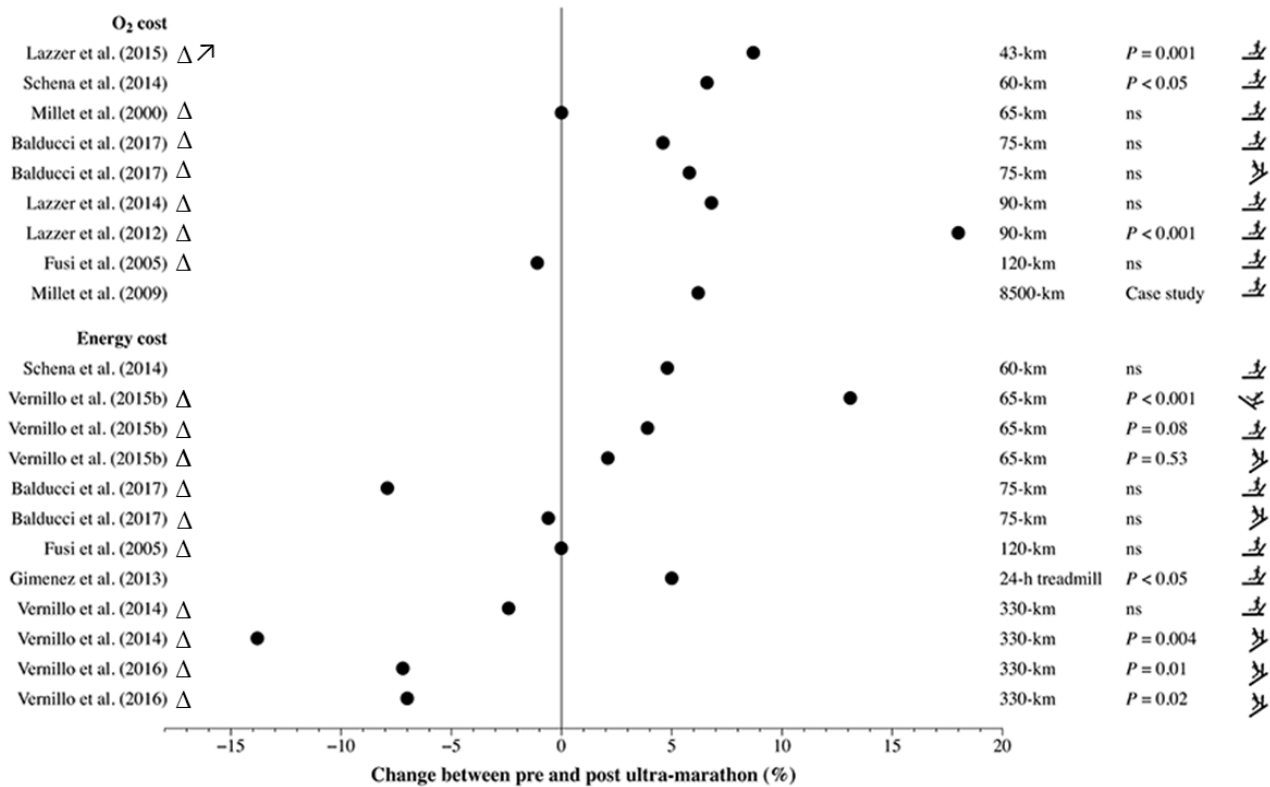


Figure 21. Summary of the studies examining the changes in running economy as O_2C or Cr after running ultra-marathons. Modified from Vernillo et al. (2017). Δ, mountain ultramarathon; ↗, uphill only race.

Other studies have used Cr instead of O_2C as their measure of running economy, while some of the studies referenced above used both measures. Balducci et al. (2017) and Fusi et al.

(Fusi et al., 2008) found similar results when measuring changes in Cr. As happened with O₂C, no significant changes were observed. Observing the results reported in the last two studies in Figure 21, it is apparent that significant decreases in Cr have been reported in the longest ultramarathons (330 km) and when measured during uphill running (Vernillo et al., 2014, 2016), while significant increases in Cr have been reported after shorter distances of 43 to 65 km or 90 km in three stages, and during level or downhill running (Lazzer et al., 2012, 2015; Vernillo et al., 2015).

4.2. Potential mechanisms of changes in running economy during prolonged running

There are several physiological changes that occur during prolonged running that could explain, at least partially, the changes in running economy after prolonged exercise, specifically after trail running races. These are likely interrelated and include fatigue induced by the exercise, biomechanical changes to the running pattern, physiological changes such as increased temperature or ventilation, etc. The aim of the following section is to review these exercise-induced changes that may affect running economy.

4.2.1. Neuromuscular fatigue

One of the most important changes that occur during prolonged exercise is fatigue. The concept of fatigue has been studied from different perspectives, including physiological, psychological, biomechanical and neural. In this section the definition proposed by McIntosh and Rassier (2002) will be used, defining neuromuscular fatigue (used here as a synonym of performance fatigability) as the progressive change that occurs in the central nervous system and/or muscles from exercise, resulting in a force output that is less than anticipated for a given voluntary contraction or stimulation. The mechanisms that lead to neuromuscular fatigue can be central (originating proximally to the neuromuscular junction, in the spinal cord or supra-spinal) and peripheral (originating distally to the neuromuscular junction, within the muscle) (Gandevia, 2001).

Central fatigue is an inability or difficulty in exciting motoneurons usually manifested by an alteration in the modulation of motoneurons discharge frequency or motor unit recruitment (Gandevia, 2001), which can be caused by various mechanisms. It can be measured through reductions in maximal voluntary activation (VA, an index of maximal central drive to the muscles).

This reduction can be caused by a decrease in motor neuron activity at the spinal level and/or, at the supraspinal level, a failure of the motor cortex to stimulate the motoneurons or by changes in feedback from the periphery. Several mechanisms have been proposed as potentially responsible for central fatigue, including changes at the supraspinal level such as the accumulation of brain neurotransmitters leading to decreased cortical-spinal excitation (Blomstrand et al., 1988; Swart et al., 2009), changes in brain concentrations of other substances such as ammonium ions (Nybo & Secher, 2004), and reductions in brain oxygenation (Nielsen et al., 1999); changes at the spinal level such as a decline in neural drive and local intrinsic adaptations of the motoneuron of peripheral inhibitory feedback mechanisms (Taylor et al., 2016); and afferent feedback from group III and IV muscle afferents (Taylor et al., 2016) which respond to changes in intramuscular metabolite concentrations and impair the output of spinal motoneurons.

Peripheral fatigue is a decrease in the ability of the muscle to produce force and power, caused by changes within the muscle. There are three primary causes of peripheral fatigue: impaired calcium release/reuptake, impaired calcium sensitivity and reduced force per cross bridge (Allen et al., 2008). In turn, several metabolic and ionic disturbances can lead to these impairments. For example, during exercise in the severe domain the sustained contribution of substrate level phosphorylation leads to an accumulation of H^+ and inorganic phosphates, which have multiple roles in impaired excitation-contraction coupling and cross-bridge function (Sundberg & Fitts, 2019). During prolonged exercise at moderate intensity glycogen depletion oxidative stress and impairments in neuromuscular propagation likely play an important role in inducing peripheral fatigue through impairments in calcium release. Evidence in support of this comes from the prolonged low frequency fatigue demonstrated following prolonged exercise (Temesi et al., 2015). Furthermore, muscle damage induced during eccentric muscle contractions associated with prolonged running can cause disruptions to structures implicated in the excitation-contraction coupling (Giandolini et al., 2016b), thereby further compounding low frequency fatigue.

Central and peripheral fatigue have been shown to occur after prolonged trail running exercise, with strength losses of the knee extensors ranging from ~15% to ~40% (Figure 22). Regarding central alterations, VA deficits between 8% and 30% for the plantar flexors and knee extensors have been reported following trail races ranging from 30 to 320 km (Giandolini et al.,

2016a). These decreases in VA show the presence of central fatigue, which may be caused by different mechanisms. However, the interpolated twitch technique with peripheral nerve stimulation, which is the most widely used method to measure VA, does not permit to distinguish between spinal and supraspinal mechanisms underlying the activation deficit (Millet et al., 2011), and the exact contribution of supraspinal and spinal factors to the reduced VA is unknown. However, mechanisms such as Ia afferent disfacilitation (Avela et al., 1999), group III/IV inhibitory feedback (Sidhu et al., 2018) and impaired motor cortical output (Espeit et al., 2021) may contribute to reduced VA. Peripheral fatigue after prolonged running has been shown by a number of experiments reporting dysfunctions of the knee extensors and plantar flexors after prolonged running. Decreases in sarcolemmal excitability, measured through reductions in M-wave as a response to a single stimulation of a relaxed muscle have been shown after trail running races (Millet et al., 2003; Saugy et al., 2013). The force response to single stimulations or high and low frequency doublets has also been observed to decrease following trail running races (Besson et al., 2020; Millet et al., 2003; Saugy et al., 2013; Temesi et al., 2015, 2021). These changes in evoked force are related to impairments in excitation-contraction coupling and/or alterations in cross bridge force capacities (Place et al., 2010).

The peripheral changes in particular may have implications for running economy. For example, peripheral fatigue could lead to the need to recruit additional motor units and less efficient muscle fibers to sustain a given running speed, therefore increasing Cr.

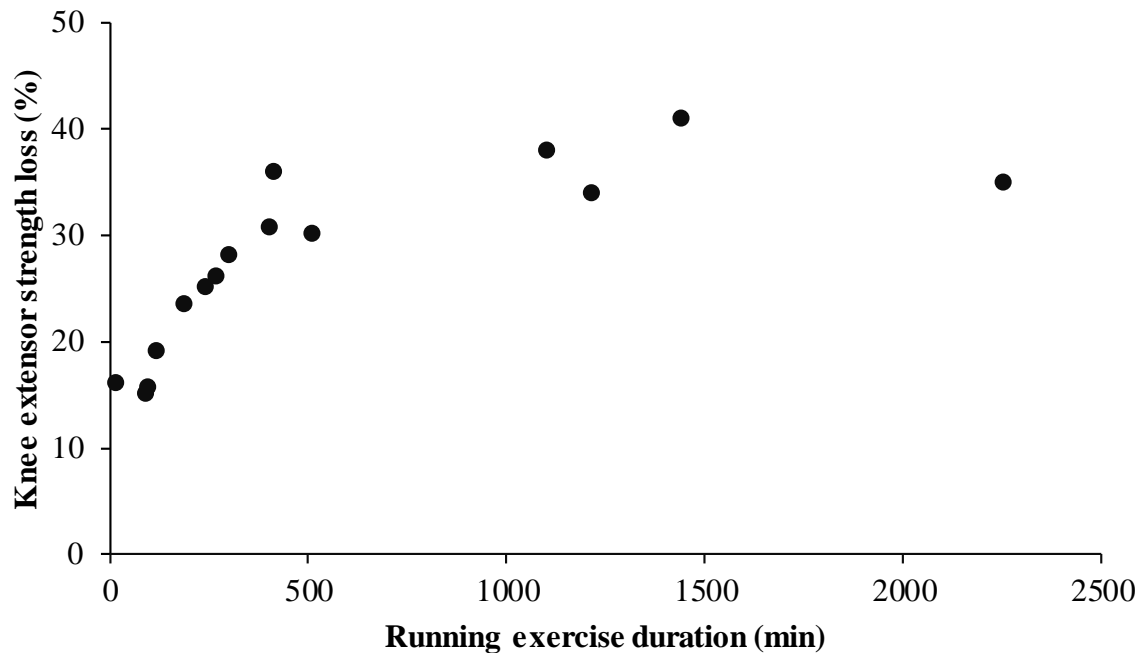


Figure 22. Knee extensor isometric strength loss from pre- to post-exercise as a function of running duration. Adapted from Giandolini et al. (2016a).

4.2.2. Body mass and load carrying

Body mass changes during trail running races, mainly due to dehydration (Coates et al., 2021). Since running economy is generally expressed as cost per unit of body mass, this may not be reflected when measuring running economy after a trail running bout. However, it is possible that despite no changes in running economy normalized to body weight, there could be a decrease in the total energy requirement of running, since the carried mass would be lighter. Furthermore, trail runners often carry equipment during the races, including water and food. These are usually carried in small backpacks or sometimes in handheld systems. Over the course of a race, athletes consume the food and liquid they carry, and they may refill several times at aid stations. These changes in carried weight can have an effect in Cr. Indeed, Scheer et al. (2019) found an increased Cr (normalized to body mass) when carrying a 3 kg backpack compared to a 1 kg backpack when running at different speeds. Therefore, decreasing the weight of the backpack overall is important to improve Cr in trail runners, with potentially greater importance at the end of the race, when some items, such as extra water or food, will not be needed to perform.

4.2.3. Biomechanical changes

Several biomechanical changes occur during prolonged trail running. Increases in step frequency have been reported after road marathons (Kyrolainen et al., 2000) and after simulated and real trail running competitions (Degache et al., 2013, 2016; Morin et al., 2011). However, after shorter duration running, such as 1-h near-maximal treadmill run, the opposite result was found, preferred stride frequency decreased significantly, with optimal stride frequency (the stride frequency that minimized $\dot{V}O_2$) decreasing in a similar fashion (Hunter & Smith, 2007). This decrease in stride frequency was accompanied by an increase in $\dot{V}O_2$ post-run, showing a potential increase in Cr, had the RER remained constant (not reported). Vertical oscillation of the center of mass and vertical stiffness have also been shown to decrease after fatiguing hilly running exercise (Degache et al., 2013, 2016; Morin et al., 2011). The changes in leg stiffness after prolonged trail running exercise seem to be more variable, since increases (Degache et al., 2013), decreases (Degache et al., 2016), and no changes (Degache et al., 2016; Morin et al., 2011) have been reported. It has been suggested that some of these changes, such as reduced stride length and increased stride frequency may be positive adaptations that improve performance in trail running by reducing peak loading forces and damage to the musculoarticular system, despite the increased Cr (Millet et al., 2012). Indeed, Millet et al. (2009) reported an increase in step frequency in a runner who completed an 8500 km run over 161 days, concomitant with a 6% increase in Cr, and they speculated that this was a mechanism to limit the mechanical consequences from the extreme running distance, despite the increase in Cr. Perhaps the opposite result, a decrease in step frequency found after a 1-h near-maximal treadmill run, matching optimal frequency as reported by Hunter and Smith (2007) shows that fatiguing exercise of less duration and without elevation changes does not have the same effect as prolonged trail running, probably because muscle damage, i.e. pain, is lower after a 1-h treadmill run. It is thus possible that the self-selected cadence is chosen to optimize Cr, instead of muscle damage and pain, but this is a speculation. Interestingly, regarding the relationship of biomechanical changes with fatigue, Morin et al. (2011) found no relationship between any of the kinematic changes after a 166 km mountain ultramarathon and the fatigue-induced loss of force in the knee extensors and plantar flexors.

4.2.4. Muscle and tendon stiffness

Changes in stiffness can occur after fatiguing exercise. For example, changes in knee extensor muscle-tendon stiffness have been observed after fatiguing exercise consisting of isometric training and stretch-shortening cycle contractions (Toumi et al., 2006). Fletcher et al. (2010) found a negative correlation between changes in Achilles tendon stiffness and changes in Cr after a training program designed to improve tendon stiffness, suggesting that higher tendon stiffness may be a beneficial for running economy. Another study from the same group (Fletcher & MacIntosh, 2018) had runners run for 90 min on a treadmill at moderate intensity (85% of their lactate threshold). They showed a significantly lower Achilles tendon stiffness following the 90 min run, and a significant negative correlation between changes in tendon stiffness and changes in Cr. They also measured a significant positive correlation between changes in Cr and changes in the estimated energy cost of the triceps surae muscles, suggesting that the lower tendon stiffness required more work to be done by the muscle, therefore increasing Cr. If 90 minutes of treadmill running caused changes in tendon stiffness, it is likely that running of longer duration and including steep uphill and downhill sections will also have a negative effect, perhaps greater, on muscle or tendon stiffness. Indeed, Andonian et al. (2016) found a decrease in quadriceps muscle stiffness after a 330 km (24000 m D+) mountain ultramarathon. This suggests that the changes in tendon stiffness after prolonged running, and specifically trail running, could be at least partially responsible for the changes in Cr.

4.2.5. Temperature

The repeated muscle contractions during exercise produce heat, which must be dissipated. The ability to dissipate the heat depends on two main factors: the rate of heat production, which depends on intensity, and the environment. Therefore, shorter endurance events may be more likely to induce hyperthermia than longer events, due to the higher intensity leading to higher rate of heat production (Bouscaren et al., 2019). At low ambient temperatures there is a high temperature gradient between the body and the air, and therefore there is more heat dissipation, whereas at higher ambient temperatures the temperature gradient is smaller, and therefore less heat is dissipated, leading to heat accumulation and therefore exercise hyperthermia. Hyperthermia also has shown to negatively affect Cr. MacDougall et al. (1974) showed significantly higher \dot{V}_{O_2C} when exercising in hyperthermic conditions compared to normal or hypothermic conditions. The authors

suggested that the increase in $\dot{V}O_2$ may be caused by an increased energy requirement for peripheral circulation, increased sweat gland activity, hyperventilation and decreased efficiency of energy metabolism. Regarding efficiency of energy metabolism, Brookes et al. (1971) showed a disruption in mitochondrial respiratory control when rat muscle mitochondria were incubated at high physiological temperatures, which led to a loss in efficiency, requiring more oxygen per unit of ATP synthesized. In contrast, Rowell et al. (1969) showed no alterations in $\dot{V}O_2$ at submaximal intensities when exercising in hyperthermic conditions. They suggested that a possible increase in the mechanical efficiency of the muscle at elevated temperatures may reduce $\dot{V}O_2$ during exercise enough to compensate the increased $\dot{V}O_2$ due to the increased cost of circulation, ventilation and sweating.

4.2.6. Cardiorespiratory changes

It has been suggested that changes in cardiorespiratory measures such as HR and \dot{V}_E are partly responsible for changes in Cr during submaximal exercise (Pate et al., 1992). Indeed, Thomas et al. (1995) found strong correlations between changes in \dot{V}_E and changes in $\dot{V}O_2$ during a 5 km run in men ($r = 0.64$, $p < 0.05$) and women ($r = 0.77$, $p < 0.0001$), suggesting that the increase in $\dot{V}O_2$ was caused by the increased O_2 cost of breathing. However, the fact that changes in both variables, \dot{V}_E and Cr, were correlated in several studies does not imply that \dot{V}_E was the cause of increased Cr. In fact, estimates of the cost of exercise \dot{V}_E have shown that the cost of \dot{V}_E increased $\dot{V}O_2$ by 0.4-0.6 ml/kg/min in men, and 0.3-0.5 ml/kg/min in women, which explained only 12-19% of the increase in $\dot{V}O_2$ for men and 16-26% for women (Aaron et al., 1992; D C Poole, 1994). This shows that \dot{V}_E only explains a small fraction of the increase in Cr after exercise, and variables other than the increase in \dot{V}_E must also play a role in the increase in Cr. Recent research by Kipp et al. (2021) measured the work of breathing using optoelectronic plethysmography. They showed that at relatively high ventilations, 75% of $\dot{V}_{E\max}$, equivalent to a \dot{V}_E of 100 ± 29 L/min and 86 \pm 6% of $\dot{V}O_{2\max}$, work of breathing was equivalent to 234 ± 24 J/min, or 3.9 ± 0.4 W. Regarding cardiac factors, it is very unlikely that changes in myocardial $\dot{V}O_2$ during exercise have a significant effect on changes in exercise Cr, since myocardial $\dot{V}O_2$ only constitutes 1-2% of whole body $\dot{V}O_2$ during exercise (Kitamura et al., 1972).

4.2.7. Changes in muscle metabolism

As previously stated, muscle fiber type may have an effect on Cr, due to the fact that type II fibers have a higher cost of ATP, and therefore O₂, to produce force. While it is extremely unlikely that muscle fiber type changes during exercise, it is well known that during fatiguing tasks there are changes in the activation of muscle fibers. While the smaller, more oxidative type I fibers are recruited preferentially at the beginning of a submaximal exercise bout, they fatigue over time, and type II fibers are recruited to maintain force production. Therefore, since type II fibers are less efficient (Reggiani et al., 2000), it is likely that there will be an increase in energy demand to generate ATP as more of them are recruited. Blood lactate concentration may also influence changes in Cr during exercise. Hoff et al. (2016) had world-class endurance athletes run at their lactate threshold speed for five minutes immediately after a two high-intensity running bouts which led to average blood lactate concentrations of 3.6 ± 0.8 or 5.5 ± 0.8 mmol/L at the start of the bout at lactate threshold speed. Cr was 5.5% higher on average after the run at 5.5 mmol/L than after the run at 3.6 mmol/L, while there were no statistical differences in HR, \dot{V}_E or RER between conditions. The authors suggested that the previous lactate concentration was the cause of the increased Cr, but it is also possible that other factors influenced the change Cr, such as greater fatigue from the more intense bout of running at 5.5 mmol/L.

Two studies were performed with the goal of investigating the effects of previous prolonged endurance exercise on C_L. Study 3 focused on the changes in Cr induced by trail running races of different distances, ranging from 40 to 170 km. Study 4 took a different approach, matching the duration and intensity of exercise during two different types of locomotion, running and cycling, which are characterized by two different types of muscle contraction. Concentric contractions are predominant in cycling, while the stretch-shortening cycle is much more predominant during running. The goal of Study 4 was to assess the differences in changes in C_L after both of these types of exercise. Furthermore, an exploratory approach was taken in both studies to identify potential causes of the changes in C_L. Other physiological, neuromuscular and biomechanical variables were measured with the goal of identifying possible causes of the changes in C_L.

4.3. Degradation of energy cost with fatigue induced by trail running: effect of distance (Study 3).

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Introduction

The popularity of trail running has increased dramatically in the last decades. According to the International Trail Running Association, a trail race is a pedestrian competition which takes place in a natural environment, with less than 20% of the course on paved roads and distances ranging from a few kilometers to 80 km and beyond for ultra-trail races (itra.run, 2020). The different races are classified in 7 categories, from XXS to XXL, according to their distance and elevation gain. Participation in these events can produce extreme levels of fatigue. Indeed, losses of maximal isometric strength ranging from 15% to 40% have been reported after trail running events (for a review see Giandolini et al. (2016)). The highest levels of strength loss have been reported for the 100 miles format, which can lead to a decrease of ~35-40% in the maximal voluntary contraction of both knee extensors and plantar flexors (Millet et al., 2011), as well as significant reductions of voluntary activation (Millet, Martin, & Temesi, 2018). This high level of neuromuscular fatigue, and, more importantly, the associated high level of soreness from lower limb tissue, could induce some of the biomechanical changes associated with these competitions.

In addition to running biomechanics, the deterioration of Cr with fatigue may be related to physiological alterations such as increased ventilation (\dot{V}_E) and changes in substrates utilisation. Indeed, increased \dot{V}_E is related to increased energy cost of breathing (Aaron et al., 1992; Margaria et al., 1960), which increases the total cost of exercise. \dot{V}_E has been shown to be correlated with increased Cr after a submaximal run (Thomas et al., 1995) and \dot{V}_E at a fixed intensity has been shown to decrease with training, and that change is related to decreased Cr (Franch et al., 1998). Endurance running has been associated with a decrease in the respiratory exchange ratio (RER) at

a given running speed, showing a greater reliance on lipids as energetic substrate for the exercise (Gimenez et al., 2013; Hausswirth et al., 1997; H. Kyrolainen et al., 2000; Vercruyssen et al., 2016; Xu & Montgomery, 1995). This suggests that a single bout of long duration exercise induces metabolic changes, that could affect the calculation of Cr, since oxidation of lipids requires more oxygen than that of CHO (Péronnet & Massicotte, 1991). Therefore, a change in oxygen consumption does not necessarily reflect a change in Cr, and this is the primary reason why it has been suggested that Cr should be calculated as energy cost, instead of oxygen cost (Fletcher et al., 2009; Shaw et al., 2014).

The deteriorated Cr with fatigue due to previous running exercise has been observed for various exercises such as 3 km high intensity efforts (Candau et al., 1998), 60 minutes bouts (Hunter & Smith, 2007) and marathon distance (H. Kyrolainen et al., 2000; Nicol et al., 2007). The interaction between the intensity of the run and its duration affects the magnitude of the changes in Cr. Higher intensity for a given duration was associated with greater increases in Cr after a 90-minute run (Xu & Montgomery, 1995). Similarly, for a given exercise intensity, Cr was shown to increase with increasing distance (Brueckner et al., 1991; Gimenez et al., 2013). However Cr was not found to increase in several studies when it was measured during submaximal low-intensity efforts of 10 km to 6 h at an intensity that could be maintained for a much longer duration (Brueckner et al., 1991; Finni et al., 2003; Gimenez et al., 2013). This suggests that a relatively high level of intensity relative to the duration of the exercise may be required to elicit changes in Cr.

The literature shows a variety of changes in Cr after trail running bouts. Vernillo, Millet and Millet (2017) reviewed the literature measuring changes in cost of running after races ranging from 43 to 330 km. Cr decreased by 7-14% after a mountain ultra-marathon of 330 km (Vernillo et al., 2016, 2014), yet Cr increased by 10% after a 43 km uphill race (Lazzer et al., 2015) and by 18% after a 90 km trail race (Lazzer et al., 2012). Other studies did not find significant differences in Cr after trail races of 65 km (Millet et al., 2000), 75 km (Balducci, Cléménçon, et al., 2017) and 120 km (Fusi et al., 2008). The discrepancy in the results reported in the literature could be partially due to the fact those studies were conducted in different races, with different courses and distances and on different terrain and conditions. To the best of our knowledge, the effect of race distance

on Cr after trail running races of different distances in similar terrain and similar environmental conditions has never been studied.

In addition to the distance, exercise intensity and terrain (i.e. treadmill vs. overground), together with the slope at which Cr is measured, may also contribute to explain the discrepancy in the literature. Since usually more than half of the time in trail running races is spent in uphill sections (Björklund et al., 2019), it is possible that uphill Cr will be a more sport-specific parameter than level Cr. Indeed, it was shown that Cr on level terrain is not correlated to cost of running at inclines of 12.5% and 25% in a group of high level trail runners (Balducci et al., 2016). Furthermore, Ehrstrom et al. (2018) found that adding Cr at a 10% incline markedly improved the power of a predictive model of performance in trail running. The model was not improved when using Cr on a flat treadmill as a predictor, suggesting that uphill Cr may be a more important factor in trail running performance. The aforementioned review from Vernillo, Millet, & Millet (2017) found decreased Cr after a trail running ultra-marathon of 330 km during uphill running, but no differences in flat condition. Cr measured after events of 43 to 140 km either increased or did not change significantly when measured during level running, and did not change significantly when measured during uphill running. This suggests that the changes in Cr after trail running races could be affected by the incline. Little data is available on the effect of fatigue on Cr at different inclines after shorter races. However, Vercruyssen et al. (2016) found that after a 18.4 km simulated race level Cr did not change, but Cr at 10% incline increased significantly.

The evidences cited above suggests that Cr may be affected by the distance of the event as well as the method of measurement (flat vs. uphill running). However, to the best of our knowledge, no direct comparisons of races run on the same terrain with similar weather conditions have been previously made. Thus, the first aim of the present study was to investigate the effect of trail running races of different distances, ranging from 40 to 170 km, on Cr. The secondary purpose was to examine whether the slope (level vs uphill running) influences the Cr changes with fatigue.

Materials and Methods

Participants

Seventy-five athletes (49 males, 26 females) participating in one of the Ultra-trail du Mont Blanc[®] (UTMB[®]) races were recruited for the study, 46 of which were able to complete the testing and were thus included in the analysis (see Figure 23). Details on participants' characteristics can be found in Table 9. All participants gave their written consent after being informed of the study procedure and the risks involved and being cleared for participation by a medical doctor. They were also allowed to withdraw from the study at will. The experiment was conducted according to the Declaration of Helsinki. Approval for the project was obtained from the French Ethical Research committee (Comité de Protection des Personnes Ouest VI). The study was registered at ClinicalTrials.gov (NCT04025138).

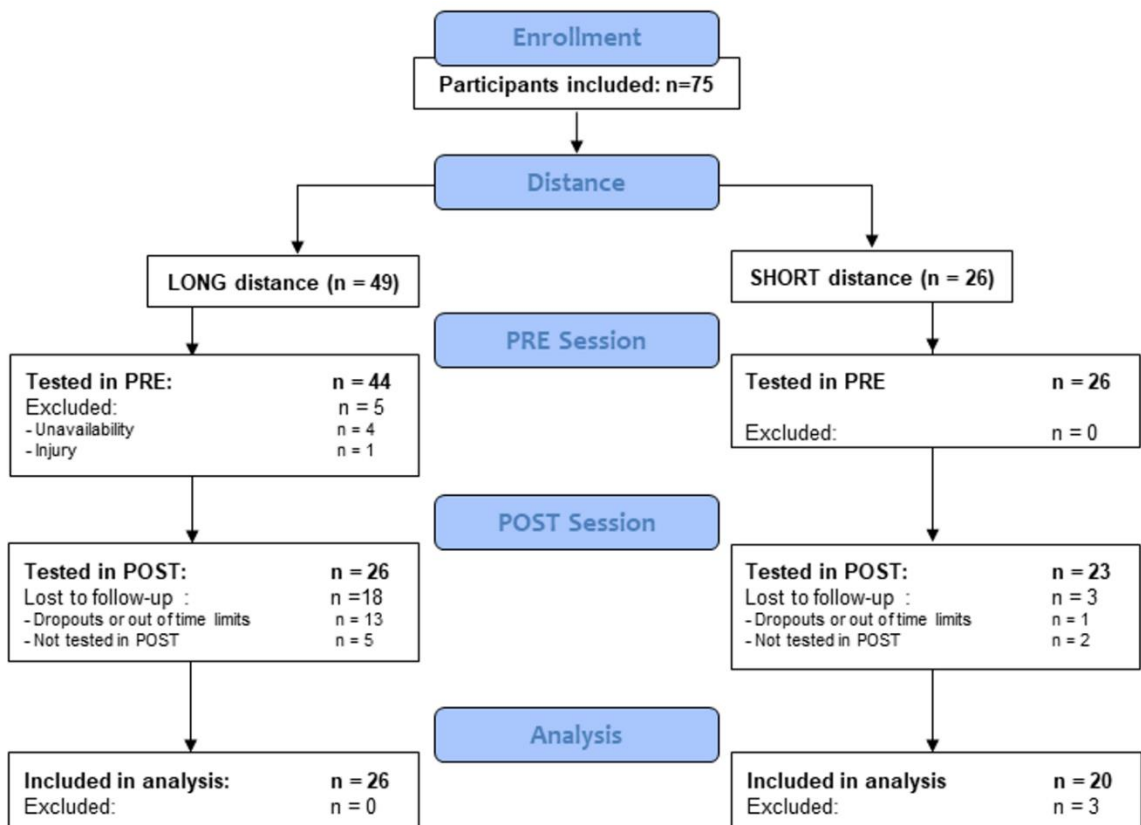


Figure 23. Inclusion chart. Participants not tested experienced extreme fatigue after the events, which did not allow them to perform the tests. Three participants were excluded from analysis due to technical issues with the testing equipment preventing data collection.

Overview

This study was part of a larger study investigating the effect of trail and ultra-trail racing on different physiological and biomechanical responses in men and women. Participants visited the laboratory three different times. Four to eight weeks before the event, each participant visited the laboratory for an inclusion visit, which included a medical test to obtain approval to participate in the study as well as a maximal exercise test and familiarisation with all the testing procedures. Twenty-four to 48 h before their race, participants visited the laboratory a second time for a Cr pre-race measurement on a level treadmill (FLAT) and at 15% incline (UH). Immediately after finishing the race, the participants were taken to the laboratory where they were seen by a medical doctor, who approved their participation in the subsequent tests. The Cr measurement was repeated during the post-race visit.

Races

Each participant competed in one of the five races at the UTMB[®]. The races were classified into SHORT (less than 100 km, 2 races) and LONG (more than 100 km, 3 races). The characteristics of each race are detailed in Table 9. Fifty-seven runners finished their respective event (32 LONG, 25 SHORT), of which 46 (17 women) were able to complete the post-test FLAT and 38 (12 women) were able to complete the post-test UH.

Data Collection

A portable, breath by breath metabolic cart (Metamax, Cortex, Leipzig, Germany) was used to measure ventilatory and gas exchange variables. The system was calibrated according to the manufacturer specifications before each test. Sample lines and turbines were changed every two tests at most, to test with clean and dry equipment, according to manufacturer specifications. Heart rate (HR) was recorded during each testing session using an HR monitor (H7, Polar, Finland).

Maximal Exercise Test

An incremental exercise test was performed to measure $\dot{V}O_{2\max}$ (4 to 8 weeks before the event). After obtaining medical clearance, the participants started the test with a 4-minute warm-up on a motorized treadmill (EF 1800, HF Tecmachine, Andrézieux-Bouthéon, France) at 10 km/h

and 0% incline. After 1 min of rest, the treadmill incline was set to 12% and the incremental test began at a speed of 5 km/h for women and 6 km/h for men. The incline was held constant and the speed was increased by 0.5 km/h every minute until the runner reached voluntary exhaustion, which occurred at speeds of 7.5 to 14 km/h.

Cost of Running Test

To measure Cr (24 to 48 h before the event), each participant ran for four minutes on a motorized treadmill (h/p/cosmos, Munich, Germany) at 0% incline and at 90% of the speed sustained during the last minute of the maximal test. After 1 min of rest each participant ran for four minutes on a 15% incline at 70% of their maximal speed during the maximal exercise test. The intensities were chosen to produce an RER below 1.0 and a steady state within 4 minutes, while allowing for a compromise to keep the participants running, and not walking, during the inclined test. A blood sample was taken from the fingertip after each bout of exercise and blood lactate concentration ([La⁻]) was analyzed using a Lactate Scout (EKF Diagnostics, Cardiff, UK). Immediately after finishing the race, the participants returned to the laboratory to perform post-race testing, during which the same protocol was repeated.

Data analysis

$\dot{V}O_{2max}$ was measured as the highest value averaged during 30 s. The maximal speed of the test was calculated as the average speed during the last minute before reaching exhaustion. Oxygen uptake, carbon dioxide production, and \dot{V}_E were measured and Cr was calculated using RER to determine the energy equivalent of oxygen. Due to the inability of an important proportion of participants to sustain the pre-set speeds during 4-minutes after the race, Cr was compared from pre to post for a 30-s period corresponding to the minutes 2:30 to 3:00 of each stage, after checking that a steady state had been achieved. Taking Cr at three minutes left 46 and 38 participants who completed at least 3 minutes of FLAT and UH running, respectively (compared to 44 and 24 if Cr was taken during the fourth minute). Some participants were observed to have a great increase in ventilation post-race compared to pre, while running at the same intensity. As a result, Cr minus the energy cost of breathing (Cr-breath) was also calculated by subtracting the work of breathing (W_B) to Cr, estimated using the equation proposed by Coast et al. (Coast et al., 1993):

$$WB = -0.251 + 0.0382 \cdot V_E + 0.00176 \cdot V_E^2$$

Statistical Analyses

The participants were split according to race distance in two groups, SHORT (races < 100 km) and LONG (races > 100 km). Data are expressed as mean \pm SD. Data were tested for normal distribution and homogeneity of variance using the Shapiro-Wilk and Levene tests, respectively. The effect of race distance on the change in Cr, \dot{V}_E , RER and $[La^-]$ was assessed using a mixed model ANOVA with two within-participants factors (time and incline) and a between-participants factor (distance). When a significant interaction effect was found, a Tuckey post-hoc test was used to identify where differences lie. Effect size was reported as partial eta squared (η_p^2) for the ANOVA tests, and when the post-hoc tests did not reveal significant differences, effect size was reported as Cohen's d. Paired t-tests were used to assess the differences between SHORT and LONG groups during the maximal test, as well as the differences between the third and fourth minutes of Cr data collection. The correlations between FLAT and UH Cr, between changes in FLAT and changes in UH Cr and between average running speed during the race and change in Cr were analysed for all athletes pooled using Pearson's product-moment correlation coefficient. Significance was set at $p < 0.05$ for all statistical tests.

Results

Maximal Exercise Test

VO_2 max was 59.9 ± 6.7 ml·kg⁻¹·min⁻¹ for LONG and 57.3 ± 17.8 ml·kg⁻¹·min⁻¹ for SHORT. The maximal speed achieved during the test was 10.7 ± 1.3 km·h⁻¹ for LONG and 9.5 ± 3.6 km·h⁻¹ for SHORT. There were no significant differences in VO_2 max or speed between groups.

Comparison between 3 min and 4 min analysis

$\dot{V}O_2$ was not significantly higher at minute 4 compared to minute 3 before the race, for both FLAT (2.17 ± 0.48 vs. 2.18 ± 0.48 L·min⁻¹, $p = 0.636$) and UH (3.09 ± 0.62 vs. 3.08 ± 0.62 L·min⁻¹, $p = 0.13$). After the races, $\dot{V}O_2$ at minute 4 was significantly higher compared to minute 3 for FLAT (2.26 ± 0.54 vs. 2.24 ± 0.54 L·min⁻¹, $p = 0.032$) and UH (3.18 ± 0.73 vs. 3.14 ± 0.73 L·min⁻¹, $p = 0.004$).

Table 9. Race details and participant characteristics

Race	Distance Classification	Distance (km)	D+ (m)	ITRA km-effort	ITRA Category	Men's Winning Time (hh:mm:ss)	Participants (N)	Age (y)	Height (cm)	Weight (kg)
MCC	SHORT	40	2,300	63	S	3:40:46	12	36 ± 9	174 ± 7	65.8 ± 9.8
OCC	SHORT	55	3,500	90	M	5:19:24	8	33 ± 8	174 ± 12	73.5 ± 10.8
CCC	LONG	101	6,100	162	XL	10:28:49	13	36 ± 8	176 ± 7	62.7 ± 10.7
TDS	LONG	145	9,100	236	XXL	18:03:06	2	40 ± 6	166 ± 15	56.1 ± 13.4
UTMB	LONG	170	10,000	270	XXL	20:19:07	11	37 ± 6	171 ± 9	63.0 ± 9.3

Table 10. Changes in Cost of running and associated physiological variables during flat and uphill running after SHORT and LONG trail running races.

		FLAT		UH		ANOVA P values (η_p^2)						
		Pre	Post	Pre	Post	Time	Distance	Incline	T × D	T × I	I × D	T × D × I
Cr (J·kg ⁻¹ ·km ⁻¹)	SHORT	4.13 ± 0.38	4.51 ± 0.36	8.78 ± 0.45	9.33 ± 0.57	< 0.001 (0.294)	0.034 (0.119)	< 0.001 (0.993)	0.029 (0.126)	0.243 (0.038)	0.252 (0.036)	0.214 (0.043)
	LONG	4.12 ± 0.35	4.24 ± 0.48	8.71 ± 0.38	8.82 ± 0.50							
Cr-breath (J·kg ⁻¹ ·km ⁻¹)	SHORT	4.05 ± 0.37	4.40 ± 0.34	8.55 ± 0.43	9.02 ± 0.53	0.004 (0.210)	0.015 (0.154)	< 0.001 (0.994)	0.017 (0.148)	0.775 (0.002)	0.179 (0.050)	0.137 (0.061)
	LONG	4.03 ± 0.33	4.12 ± 0.46	8.47 ± 0.35	8.47 ± 0.48							
\dot{V}_E (L·min ⁻¹)	SHORT	56.8 ± 12.9	65.5 ± 14.6	82.1 ± 15.3	94.9 ± 20.2	< 0.001 (0.655)	0.054 (0.099)	< 0.001 (0.909)	0.114 (0.068)	0.007 (0.186)	0.461 (0.015)	0.61 (0.007)
	LONG	64.3 ± 14.0	77.3 ± 18.7	90.9 ± 20.3	109.8 ± 25.9							
RER	SHORT	0.86 ± 0.03	0.75 ± 0.03	0.96 ± 0.03	0.86 ± 0.04	< 0.001 (0.918)	0.051 (0.102)	< 0.001 (0.921)	0.022 (0.138)	0.005 (0.202)	0.156 (0.055)	0.162 (0.054)
	LONG	0.84 ± 0.04	0.75 ± 0.03	0.92 ± 0.03	0.85 ± 0.04							
[La ⁻] (mmol·L ⁻¹)	SHORT	2.68 ± 1.68	2.37 ± 0.88	5.01 ± 1.68	3.67 ± 1.51	0.867 (0.001)	0.962 (0.001)	< 0.001 (0.664)	0.001 (0.316)	0.217 (0.052)	0.923 (0.001)	0.088 (0.097)
	LONG	2.11 ± 0.69	2.87 ± 0.99	3.88 ± 1.18	4.68 ± 1.28							

Ventilation and RER

\dot{V}_E showed a significant time effect ($p < 0.001$, $\eta_p^2 = 0.655$) increasing by $18.6 \pm 16.3\%$ and $18.8 \pm 15.7\%$ after the races for FLAT and UH, respectively. There was a significant effect of incline, with \dot{V}_E higher during UH compared with FLAT. There was no time \times distance interaction, but there was a time \times incline interaction. The post-hoc test revealed that both FLAT \dot{V}_E and UH \dot{V}_E were significantly higher post-race than pre-race (Table 10). There was a significant effect of time on RER ($p < 0.001$, $\eta_p^2 = 0.918$), which decreased significantly after the races. There was a significant time \times distance interaction ($p = 0.022$, $\eta_p^2 = 0.138$), and post-hoc testing revealed significant differences between Pre-SHORT and Pre-LONG ($p = 0.021$), between Pre-SHORT and Post-SHORT ($p < 0.001$), and between Pre-LONG and Post-LONG ($p < 0.001$). There was a significant time \times incline interaction, and post-hoc testing revealed significant differences between Pre-FLAT and Post-FLAT, as well as between Pre-UH and Post-UH ($p < 0.001$).

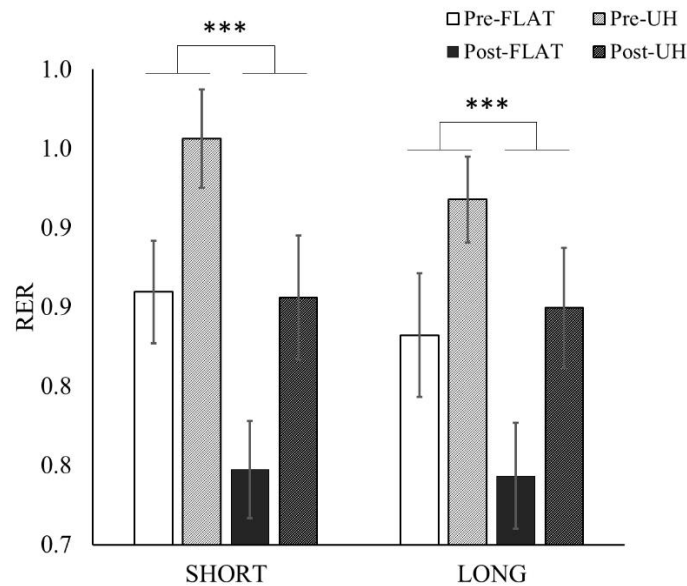


Figure 24. Respiratory exchange ratio (RER) before and after SHORT and LONG trail running races in level (FLAT) and uphill running (UH). ***, $P < 0.001$ from Pre to Post race.

Energy cost of Running

Cr showed significant effects of time ($p < 0.001$, $\eta_p^2 = 0.294$), distance ($p = 0.034$, $\eta_p^2 = 0.119$), and incline ($p < 0.001$, $\eta_p^2 = 0.993$) as well as a time \times distance interaction ($p = 0.029$, $\eta_p^2 = 0.126$). Post-hoc testing showed that Cr was increased significantly from Pre-SHORT to Post-SHORT ($p < 0.001$), but there were no significant changes after LONG distance races (Figure 25).

Cr-breath showed significant effects of time ($p = 0.004$, $\eta_p^2 = 0.210$), distance ($p = 0.015$, $\eta_p^2 = 0.154$), and incline ($p < 0.001$, $\eta_p^2 = 0.994$), and a time \times distance interaction ($p = 0.017$, $\eta_p^2 = 0.148$). Similarly to Cr, Cr-breath was significantly higher post-SHORT compared to pre-SHORT, but there was no significant effect after LONG distance races (Table 10).

FLAT Cr at rest was significantly correlated to UH Cr at rest ($r = 0.51$, $p < 0.001$, Figure 26a) and the percentage change in FLAT Cr was significantly correlated to the percentage change in UH Cr ($r = 0.75$, $p < 0.001$, Figure 26b). Cr correlated with absolute race speed for both FLAT ($r = 0.408$, $p = 0.005$) and UH ($r = 0.393$, $p = 0.016$). The correlation with speed relative to vPeak was lower for FLAT Cr ($r = 0.360$, $p = 0.018$), and non-significant for UH Cr ($r = 0.282$, $p = 0.095$).

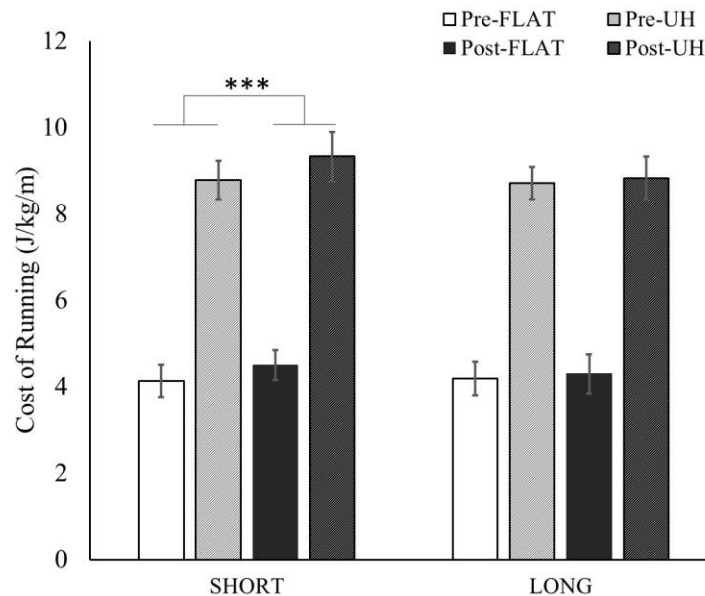


Figure 25. Changes in cost of running (Cr) during level and uphill running after SHORT and LONG distance trail races. ***, significantly different from Pre, $p < 0.001$.

Blood Lactate Concentration

There was a significant time \times distance interaction effect on blood lactate concentration $[La^-]$ ($p < 0.001$, $\eta_p^2 = 0.316$, Table 10). Post-hoc testing did not reveal significant differences between conditions, but lactate tended to be lower Post-SHORT, compared to Pre-SHORT ($p = 0.057$, Cohen's $d = 0.513$). There was an incline effect ($p < 0.001$, Table 10).

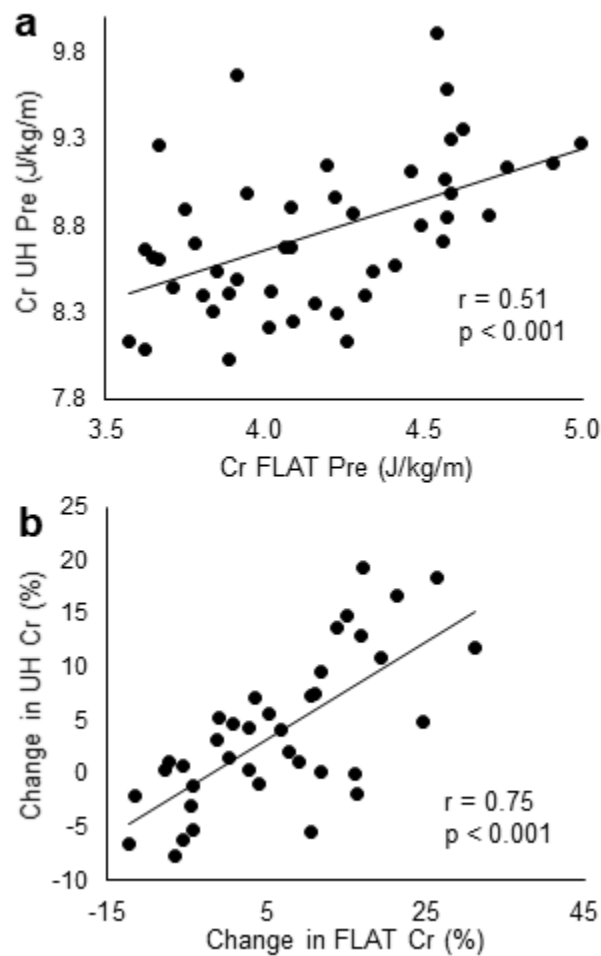


Figure 26. Relationship between pre-race level (FLAT) and uphill (UH) cost of running (Cr) (a) and relationship between change in FLAT Cr and changes in UH Cr (b).

Discussion

The goal of this study was to investigate the effects of trail running distance on Cr. The main results were i) Cr increased after short distance trail, but not after ultra-trail running races (longer than 100 km), ii) there was a significant correlation between the changes in FLAT Cr and the changes in UH Cr.

Energy cost of running

The present study was the first to directly compare the influence of trail running distance on the same terrains with similar weather conditions on Cr. A counterintuitive effect of distance was found, with the change in Cr greater after the short compared to the longer and more difficult races, and Cr increasing significantly only after SHORT, as shown in Figure 25. This study provides new and meaningful data on the effects of trail races of different distances on Cr, as the literature on this subject was at present unclear. Vernillo, Millet and Millet (2017) reviewed the studies that measured the effect of ultramarathon races on running economy, measured as oxygen cost of running or Cr. Interestingly, they found significant decreases in Cr in studies done on a mountain ultramarathon of 330 km. In more 'classic' trail running races, i.e. 43 km to 120 km, it was found that either there were no significant changes in Cr, or Cr increased after the event. It is possible that shorter races have a greater negative impact on Cr compared to longer races, possibly due to the greater intensity at which they are run. Gimenez et al. (2013) found that during a 24 h self-paced treadmill trial Cr increased after 8 h compared to baseline, but did not increase further, as runners decreased their speed to be able to complete the run. Interestingly, the increase in Cr was positively correlated with the relative intensity, expressed as percentage of the velocity associated with $\dot{V}O_2\text{max}$, which suggests that higher running intensity could be related to greater impairments in Cr. Other studies have shown that running at a higher intensity for a given duration leads to greater increases in Cr (Xu & Montgomery, 1995). The greater increase in Cr after SHORT races could be caused by the higher intensity at which they are run, possibly leading to greater muscle damage, substrate depletion and changes in running pattern, all of which could negatively affect Cr. Indeed, a significant correlation was found between race speed and change in Cr. The correlation between changes in Cr and neuromuscular fatigue (loss of maximal isometric force) in the knee extensors and plantar flexors was also assessed, and no significant correlations were found (data not shown).

Increased \dot{V}_E (see below) has been shown to be one of the contributors to increased Cr after exercise, due to the increase in energy consumption of the respiratory muscles (Aaron et al., 1992; Margaria et al., 1960; Thomas et al., 1995). The increased cost of breathing did not explain the difference in Cr between our SHORT and LONG participants in our study, since \dot{V}_E did not increase more after SHORT than after LONG. Indeed, Cr-Breath followed the same pattern as Cr, increasing significantly after the SHORT races and not after LONG races.

The role of \dot{V}_E

\dot{V}_E at a fixed running speed increased dramatically after all races, independently of distance, by an average of ~19%. Changes in \dot{V}_E at a given speed after trail running races of 60-330 km have been previously reported from non-significant changes (Gimenez et al., 2013; Schena et al., 2014) to an increase of ~18% (Millet et al., 2000; Vernillo et al., 2014). One possible cause for this increase in \dot{V}_E could be an exercise-related impairment of the pulmonary function. It has been reported that a mountain ultramarathon led to decreased vital capacity, maximal ventilation, and maximal inspiratory and expiratory pressure (Vernillo et al., 2015; Wütrich et al., 2015). Those changes in pulmonary function could potentially lead to increased \dot{V}_E during the effort to compensate for the losses of lung function. The increase in \dot{V}_E could also be caused by changes in glycogen stores. Indeed, Hugues, Turner and Brooks (1982) found that repeating a maximal exercise cycling test after a period of glycogen depletion increased \dot{V}_E for a given intensity, while decreasing blood lactate concentration. However, the fact that the increase in \dot{V}_E was comparable between LONG and SHORT, despite potentially greater glycogen depletion in SHORT (see next section), does not support the assumption that increased \dot{V}_E was mainly caused by glycogen depletion. There are other mechanisms by which exercise could drive an increase in ventilation. It has been suggested that respiratory muscles and the carotid bodies can sense changes in metabolite concentration, such as CO₂ and hydrogen ions, and increase the work of breathing muscles by redistributing blood flow (Dempsey, 2012). However, in our study \dot{V}_E increased in SHORT while there was a decrease in blood lactate concentration and therefore, presumably, a lower hydrogen ion concentration. It has also been suggested that the increase in ventilation is caused by feedback from group III and IV afferent fibers, which respond to mechanical and chemical stimuli in the locomotor muscles (Amann et al., 2010; Dempsey, 2012). It is possible that inflammation due to muscle damage caused an increase in afferent feedback, driving the increase in \dot{V}_E . Finally, it has also been suggested that increased \dot{V}_E could be caused by increase central nervous drive, increasing the firing rate of the motor neurons to the locomotor muscles and the respiratory muscles in parallel (Forster et al.,

2012). In our study, the post-race fatigue of the locomotor muscles possibly required greater neural drive to run at the imposed intensity, driving a parallel increase in \dot{V}_E .

RER and Blood Lactate

RER decreased for both groups in FLAT and UH after the events and $[La^-]$ tended to decrease for SHORT during both FLAT and UH running, but increased, non-significantly, for LONG. The decrease in RER suggests an increased reliance on lipids as energy sources for exercise. A change in RER from 0.86 to 0.75 reflects an increase in fat use from 45% of the energy coming from lipids to 83%. It has been previously observed that exercise performed in a glycogen depleted state produces lower RER and $[La^-]$ values at a given intensity (Heigenhauser et al., 1983; Hughes et al., 1982). Our findings could be caused by greater glycogen depletion in the locomotor muscles in SHORT, possibly caused by racing at a higher intensity, leaving less fuel for glycolysis and increasing the use of lipids as energy substrate.

Despite the potential role of glycogen depletion in the reduction of RER and $[La^-]$ after SHORT, this does not explain the lack of change in $[La^-]$ after LONG, despite a decrease in RER. As runners participating in LONG races had a significantly lower RER during uphill running before the races, they would have used more lipids at a given intensity, in addition to completing the race at a relatively lower intensity. Consequently, runners in the LONG races likely relied more on lipid metabolism during the event, thereby sparing glycogen stores, and attenuating glycogen depletion during the race. Furthermore, the lower intensity at which participants ran during the LONG events could also have permitted the ingestion of more CHO during the race, allowing them to spare more glycogen. In turn, a greater ingestion of CHO could have contributed to the smaller change in RER compared to SHORT, and attenuated glycogen depletion to permit a greater contribution of glycolysis and lactate production after the event. Interestingly, SHORT races had a duration of 4.5 to 12 h while LONG races had durations longer than 15 h, and it is worth mentioning that Gimenez et al (2013) found that RER decreased significantly after 8 h of running, and then it stabilised as the participants decreased their running speed for the last 16 h. This, together with our results, may suggest that there is a limit duration beyond which RER does not further decrease. Our results suggest that changes in substrate utilisation or lactate production are not the cause of changes in Cr after trail running races.

Flat vs Uphill measurement of Cr

A significant correlation was found between changes in FLAT Cr and UH Cr (Figure 26). Yet, there was no time \times incline interaction on Cr, and our data therefore does not support the hypothesis of incline having an effect on changes in Cr. Greater increases in Cr on FLAT compared to UH running after trail running events have been previously reported in the literature. For instance, Vernillo et al. (2015) measured changes in Cr while running FLAT and UH at +5% after a 65 km trail race and found that the changes in flat Cr was greater than uphill. After a 330 km ultramarathon, Vernillo et al. (2014) found a significant decrease in Cr during UH running, but not during level running. This suggests that the fatigue induced by trail running competitions could have a different effect in UH compared to FLAT Cr. These differences could be caused by the more concentric nature of the muscle contractions during uphill running compared to level running. It is possible that the greater eccentric component during level running induced more pain at each step after the race compared to uphill running. However, the present findings contrast with the results obtained by Vercruyssen et al. (2016), who found increased Cr after an 18.4 km race only in the UH running condition, and no significant changes in level Cr, suggesting that the effect of shorter trail races on level and UH Cr could be different than that of trail races of 40 km and longer. The reasons for this discrepancy are unclear.

Limitations

One of the main limitations of our study was trying to ensure that all participants were running at a similar relative intensity during Cr measurements. The maximal test that was used to set the intensities was done only once, at 12% incline, while the measurement of cost of running was done at 0% and 15% incline. To set the intensities, percentages (90% and 70% for FLAT and UH, respectively) of the maximal speed achieved during the test were used to try to ensure that participants would run at an RER lower than 1.0 and achieve steady state. This method of setting the intensity could have led to heterogenous physiological responses between participants (Iannetta, Inglis, et al., 2019). The intensity of UH running was relatively higher than that of FLAT for all participants, as measured by $\dot{V}O_2$ and RER. This is because participants were required to run (as opposed to walk) during the test, so a sufficiently fast speed to allow running was required. This higher intensity during UH compared to FLAT may explain the effect of incline on all the variables we measured (Table 10). To allow for everyone to run at the same percentage of their maximal speed whilst ensuring that the least fit participants were running during the test, the UH test speed had to be set at a higher relative intensity than FLAT. Furthermore, due to the inability of many of the participants to complete

the 4 minutes of running after the race, the measuring period had to be shortened to 3 minutes. This led to significantly lower $\dot{V}O_2$ values during the measuring period, from 2:30 to 3:00, than during the last minute in those participants who were able to finish 4 minutes of running. However, even if significant, those differences were smaller than 50 ml/min (i.e. 1%), and changes in $\dot{V}O_2$ as high as 150 ml/min and 10% have been previously used in the literature as the limit of steady state (Gruber et al., 2013). Thus, a quasi-steady state was assumed at minute 3 to calculate Cr.

Another limitation of our study is that, being part of a bigger study, there was a delay of 80 ± 19 minutes between the end of the race and the beginning of the Cr test, as the participants underwent other tests (neuromuscular function, for example) before the assessment of Cr. This could affect our results, as this period of rest could change their Cr as well as their substrate use, since they had some time to eat and digest after the race. Another issue was that some of the participants arrived in a state of extreme fatigue after more than 30 h of racing, which did not allow them to complete our tests for safety reasons. In other words, the more fatigued participants may not have been tested which may underestimate the effects of fatigue on Cr.

Conclusion

The present study adds to the literature on the effect of fatigue on efficiency after prolonged to extreme exercises. Cr increased after short trail races (40-55 km) but not after longer races (100-170 km). Further studies should investigate the reasons behind this finding but it is likely that the higher intensity at which short races were run plays a key role. The change in Cr measured during level running was significantly correlated to the change in Cr measured during uphill running, suggesting that biomechanical changes may not play a major role in deteriorated energy cost after trail and ultra-trail running.

4.4. Changes in cost of locomotion after endurance running vs cycling exercise matched for intensity and duration (Study 4).

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Introduction

The capacity to sustain the highest level of power or velocity defines performance in endurance events. The three main factors that explain performance in this type of exercise are the maximal uptake ($\dot{V}O_{2max}$), the fraction of the $\dot{V}O_{2max}$ which can be sustained during the event, and the cost of locomotion (C_L) (di Prampero et al., 1986). In running (Conley & Krahenbul, 1980) and cycling (Edward F. Coyle et al., 1992), exercise economy can vary around 20 % between participants exercising at a given intensity.

C_L is expressed in different ways depending on exercise modality. For example, in cycling, gross efficiency is usually used to quantify the ability to convert metabolic power (P_{met} ; the rate of energy consumed per unit of time exercising at a given intensity) to external mechanical power, expressed as the percentage of P_{met} that is converted to mechanical power. During running, a much more complex movement compared to cycling, mechanical power is difficult to quantify accurately. Therefore, C_L in running is often quantified as the amount of energy expended to cover a given distance (cost of running: Cr). However, to compare two different exercise modalities, C_L should be expressed in the same units. P_{met} has been used to compare cycling and running C_L in endurance athletes (Swinnen et al., 2018). Indeed, if the intensity remains constant, an increase in P_{met} implies an increase in C_L , since energy consumption has to increase to sustain exercise intensity.

C_L is influenced by endogenous (e.g., type of substrate, core temperature, ventilation) and exogenous (e.g., surface or equipment) factors (Barnes & Kilding, 2015b). An important component that influences C_L is previous exercise. Increases in C_L during cycling have been shown after 20 min of exercise at 65% and 80% of $\dot{V}O_{2max}$ (Hagberg et al., 1978), 45 minutes of moderate intensity exercise (Hagan et al., 1992), 60 min at 60% of maximal aerobic power (Passfield & Doust, 2000) and two hours of exercise at 60% (Hopker et al., 2017) and 65% (Lepers et al., 2000) of maximal aerobic power. In running, the effect of previous exercise on

running economy is less clear and it seems to depend on duration, intensity, or the combination of both (Gimenez et al., 2013; Sabater Pastor et al., 2021). It has been shown that C_L increases with time during running efforts of 3 km (Candau et al., 1998) at high intensity, 60 min at maximal sustainable speed (Hunter & Smith, 2007), and a marathon (H. Kyrolainen et al., 2000; Nicol et al., 2007). For a given running duration, greater intensity is associated with greater increases in C_L (Xu & Montgomery, 1995). Other acute metabolic and cardiorespiratory changes are observed during prolonged cycling and running exercise, (Davies & Thompson, 1986; Hopker et al., 2017; H. Kyrolainen et al., 2000; Schena et al., 2014) such as heart rate (HR) increasing due to cardiovascular drift, an increase in ventilation (\dot{V}_E) and changes in substrate utilization, shown by a decrease in the respiratory exchange ratio (RER).

For C_L calculations to be valid exercise intensity should be sub-maximal, since adenosine triphosphate resynthesis through oxidative phosphorylation must account for all of the energy consumption and this only happens below the severe intensity domain (Svedahl & MacIntosh, 2003). Furthermore, to compare two exercise modalities the relative intensity should be equivalent in both, falling within the same intensity domain, to ensure a similar metabolic disturbance in both exercise modalities. Prescribing intensity as a percentage of a maximal measure such as maximal aerobic power or $\dot{V}O_{2max}$, as previous research has done (Hagberg et al., 1978; Hopker et al., 2017; Passfield & Doust, 2000; Xu & Montgomery, 1995), may put participants in different intensity domains (Iannetta, Inglis, et al., 2019), leading to different levels of metabolic disturbance, because the metabolic response at a given intensity relative to maximal aerobic power or $\dot{V}O_{2max}$ differs between exercise modalities (Millet et al., 2009) and between participants in the same modality (Iannetta, Inglis, et al., 2019). Therefore, prescribing the intensity relative to a physiological threshold allows us to ensure that the metabolic stress is similar in both modalities and for all participants, permitting a valid comparison between changes in C_L with running and cycling.

To the best of our knowledge, no study has compared the changes in exercise economy between cycling and running after a bout of endurance exercise of the same duration at the same relative intensity. Only one study has compared the influence of an ultra-endurance event on running and cycling, finding that cycling, but not running C_L was altered (Millet et al., 2000). However, the endurance event in that study was a trail running race (65 km with 2500 m of elevation). Therefore, it is not known if running and cycling have the same effect on the C_L measured in the same exercise modality. Furthermore, although there are several factors that may influence C_L , including cycling cadence, (Ettema & Loras, 2009) running biomechanics

and changes in physiological variables such as ventilation,(Barnes & Kilding, 2015b; Saunders et al., 2004) the mechanisms that determine the changes in C_L during running and cycling are not known. The aim of this study was to compare the effect of two endurance exercises (cycling vs running) at matched intensity relative to the modality-specific GET and duration on changes in C_L . The study hypothesis was that cycling would induce a greater increase on C_L than running. A secondary aim of this study was to investigate if the changes in C_L were related to changes in other variables such as cardiac and ventilatory responses, changes in substrate utilization, blood lactate concentration, neuromuscular fatigue and perceived exertion.

Methods

Overview

The study consisted of four visits to the laboratory. During the first visit, each participant was examined by a medical doctor who approved the inclusion in the study. Subsequently, each participant completed an incremental test to exhaustion in cycling or running (randomized order), which was used to determine the intensity of the 3-h trial, followed by a familiarization with all the neuromuscular testing procedures. The second visit was used to perform an incremental test in the other exercise modality. Visits 3 and 4 were used for the 3-h trials, in the same order as visits 1 and 2. During visits 3 and 4 C_L was measured at the beginning, middle and at the end of each trial.

Participants

Nineteen male endurance athletes were recruited for this study, out of which 17 (age 33.2 ± 8.0 years, height 178.1 ± 5.7 cm, mass 72.1 ± 5.3 kg) were able to complete all four visits. All participants obtained medical approval for participation during their first visit to the laboratory, and provided written consent after being informed of the study procedure and the risks involved. This study was conducted according to the Declaration of Helsinki, and approval for the project was obtained from the Comité de Protection des Personnes Ouest IV-Nantes, France, n°55/20_1.

Maximal Exercise Tests

A treadmill (CMTD20, Laroq, La Roque d'Antéron, France) or cycle ergometer (SRM SmartIT, SRM International, Jülich, Germany) maximal exercise test was performed to determine the intensity for the constant load fatiguing trials. The protocol was similar for both tests, despite the different exercise modality. Both tests started with a 2-minute baseline, consisting of pedaling at 20 W or walking at 4 km/h, followed by a 6-minute step in the moderate intensity domain, at 120 W or 8.5 km/h. After another 4 minutes of baseline, participants performed a 30-second step incremental test, starting from 50 W in cycling or 7 km/h in running, and increasing the intensity by 15 W or 0.5 km/h every 30 s, and continued until exhaustion. If participants reached 20 km/h during the running test, the incline of the treadmill was increased by 1% every 30s until exhaustion. All participants received strong verbal encouragement during all tests. Gas exchanges were measured using a metabolic cart (Metamax 3B, Cortex, Leipzig, Germany).

The highest $\dot{V}O_2$ value recorded during 30 s was taken as $\dot{V}O_{2max}$. The gas exchange threshold (GET) was calculated from ventilatory and gas exchange data by identifying the point at which $\dot{V}CO_2$ started to increase in relation to $\dot{V}O_2$, coinciding with an increase in the ventilatory equivalent of $\dot{V}CO_2$ and end-tidal pressure of O_2 (Beaver et al., 1986). Then, to find the equivalent steady-state power or running speed at the $\dot{V}O_2$ corresponding with GET, the mean response time (MRT) was calculated for each exercise trial. Briefly, the incremental test $\dot{V}O_2$ data was fitted from the onset of the systematic rise of $\dot{V}O_2$ to the previously established GET, using a linear fit. Then, the average $\dot{V}O_2$ of the last 2 min of the moderate step was used to identify the corresponding power or speed during the incremental exercise. The difference in watts or km/h between the moderate step and the incremental test was calculated as the MRT, corresponding to the equivalent steady state work rate to $\dot{V}O_2$ relationship (Iannetta, Murias, et al., 2019). Power and speed at GET were calculated by subtracting the MRT from the power or speed at GET during the incremental test.

Constant Load Trials

Constant load trials were performed during visits 3 and 4. Each constant load trial aimed for 3 h of exercise. Seven minutes were added to the protocol to account for pauses to place and remove the equipment for ventilatory and gas exchange measurements. The chosen intensity for the constant load trials was 105 % of the power or speed corresponding to GET. This intensity was chosen after pilot testing, with the goal of choosing an intensity that would

produce fatigue, but that all participants would be able to sustain for 3 hours, and it was selected relative to the individual GET in each specific modality to ensure that all participants would experience a similar metabolic disturbance in both exercise modalities. Five participants were not able to sustain the imposed power or speed during the first trial they performed, due to muscular or joint issues, and the intensity was dropped by an average of $11.3 \pm 4.5\%$ for the rest of the trial. However, the intensity was brought back to the pre-set speed/PO during the time at which all measurements took place (see below). The intensity during the second trial was modified by the same percentage and at the same time-points, except for one subject, for whom the intensity had to be dropped during the second trial (running), with his average intensity over the 3 h being 97.6% of the predetermined intensity. Gas exchanges were measured at three different points for each trial (Start, Mid, End), as well as heart rate, blood lactate concentration and rating of perceived exertion (RPE) using the modified Borg 1-10 scale. Cycling power and cadence were measured using a power meter (SRM Science, SRM International). Running biomechanics were measured at the selected speed for the test at three time points: immediately before the start, at mid-point (75 to 80 min) and at the end of the test (165 to 170 min).

Gas Exchange Measurements

Metabolic energy cost of locomotion was measured for cycling and running using a metabolic cart. Measurements were taken at three time points for each trial, from the onset of exercise to minute 10, from minute 80 to minute 90 and from minute 170 to minute 180. The average of the last two minutes of each measurement was used to calculate C_L from $\dot{V}O_2$ and $\dot{V}CO_2$, with the energy equivalent of O_2 calculated from the respiratory exchange ratio (RER) (Péronnet & Massicotte, 1991). C_L was expressed as metabolic power (P_{met} , joules of energy spent per second) and relative to body weight, dividing cycling P_{met} by the mass of the subject before the 3 h trial, and running P_{met} by the mass of the subject at the time of each measurement. This was done because cycling is not a weight-bearing exercise, while running is weight-bearing and the change in cost of locomotion could be influenced by changes in body weight during running. Minute ventilation (\dot{V}_E) was also measured using the metabolic cart. Carbohydrate (CHO) and lipid utilization were calculated from RER and the energy equivalent of oxygen (Péronnet & Massicotte, 1991). The calculations assumed that the percentage of energy derived from protein was negligible, since it was not possible to measure the nitrogen content of urine.

Blood Lactate Concentration

After 10 (Start), 80 (Mid) and 170 (End) minutes of exercise, a blood sample was taken from the fingertip and analyzed to measure lactate concentration (Lactate Scout, EKF diagnostics, Cardiff, UK).

Neuromuscular Fatigue

Maximal voluntary contraction (MVC) of the knee extensor muscles (KE) was assessed prior to each trial, and after 3 h. KE torque was measured on an isometric knee dynamometer (ARS dynamometry; SP2 Ltd, Ljubjana, Slovenia) with the hips and knee at 90° of flexion. During each neuromuscular assessment participants performed a 3-s MVC of the right knee extensors. The percentage change in MVC was recorded as measures of fatigue.

Force-Velocity Profile

Immediately before each of the 3-h testing sessions and within 3 minutes of the end of exercise, participants' force-velocity profile was assessed by a 6-s sprint (Koral et al., 2021) on a cycle ergometer (Monark, Vansbro, Sweden) which measured friction forces, using a strain gauge (FN 3030 type; FGP Instrumentation, Les Clayes-sous-Bois, France), and flywheel displacement, using an optical encoder (Hengstler, type RI 32.0; Aldingen, Germany). The resistance on the ergometer for the first sprint was set at 0.7 N/kg of body mass, and for the post-trial sprint the resistance was adjusted proportionally to the loss of maximal isometric force. The torque and power produced were measured during each pedal stroke, and the plotted against angular velocity of the crank to determine the relationships between velocity and force or power. The parameters of the force velocity profile (v_0 and F_0) were extrapolated from the linear relationship between velocity and force, and maximal power (Pmax) was calculated as from v_0 and v_0 as:

$$P_{\max} = F_0 \times v_0 / 4$$

Running Biomechanics

Running biomechanics were measured in a force-plate equipped treadmill (Adal, Andrezieux Boutheon, France). At the designated time for the measure (after 75 and 165 minutes of running) runners left the treadmill in which they were running and walked ~20 seconds to the force-plate equipped treadmill. Then runners stood on the treadmill and their weight was measured by the force plates. The speed of the treadmill was increased immediately

to the pre-set running speed. Runners ran for 5 minutes, and a recording of the impact forces was performed during 30-s at a random point during the last of the 5 minutes, without giving notice to the participant. From the impact forces, step frequency was calculated.

Statistical Analysis

All data are presented as Mean \pm SD. The normal distribution for all variables was assessed using the Shapiro-Wilk test. A repeated measures ANOVA with two factors, time and modality, was used to assess differences in C_L , as well as RER, ventilation and HR in absolute terms and relative to peak HR in the corresponding modality. When significant effects were found, a Tukey post-hoc correction was applied. Differences between variables obtained from the maximal exercise test were assessed with a Student's t-test. Correlations between changes in C_L and physiological, neuromuscular fatigue and biomechanical variables were assessed using Person's correlation coefficient. Statistical analyses were performed using jamovi 1.2 (the jamovi project) and the threshold for significance was fixed at $p < 0.05$.

Results

Maximal Exercise Tests

There were no differences in $\dot{V}O_{2\max}$ between cycling ($61.6 \pm 6.2 \text{ mL}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$) and running ($60.7 \pm 5.4 \text{ mL}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$). $\dot{V}O_2$ at GET was significantly smaller during cycling compared to running for both absolute and relative values ($p < 0.001$). Whereas HR_{max} was smaller for cycling compared to running ($p = 0.001$), peak blood lactate concentration was greater for cycling compared to running ($p = 0.018$, Table 11).

Table 11. Maximal exercise test results in cycling and running.

	Cycling	Running	
$\dot{V}O_{22\max}$ (mL·kg ⁻¹ ·min ⁻¹)	61.5 ± 6.2	60.7 ± 5.4	
$\dot{V}O_{2\max}$ (L·min ⁻¹)	4.43 ± 0.47	4.35 ± 0.39	
GET (mL·kg ⁻¹ ·min ⁻¹)	36.5 ± 4.0	39.1 ± 3.3	***
Relative GET (%)	59.3 ± 3.5	64.6 ± 3.1	***
HRmax	181 ± 10	185 ± 11	***
Peak Lactate Concentration	13.4 ± 2.0	11.9 ± 2.6	*

Differences between running and cycling: *, $p < 0.05$; ***, $p < 0.001$; $\dot{V}O_{2\max}$, maximal oxygen uptake; $\dot{V}O_2$, oxygen uptake; GET, oxygen uptake at the first ventilatory threshold; Relative GET, oxygen uptake at the first ventilatory threshold relative to maximal oxygen uptake; HRmax, maximal HR.

Cost of Locomotion

C_L results are shown in Figure 27. Considering the absolute metabolic power, there was a significant time effect ($F = 12.82$, $p < 0.001$, $\eta^2_p = 0.445$), as well as a time × modality interaction ($F = 14.93$, $p < 0.001$, $\eta^2_p = 0.483$) for C_L . Post-hoc analysis revealed that C_L did not change during the running trial, but increased significantly during the cycling trial between Start and Mid ($p = 0.006$) and then increased further between Mid and End ($p = 0.020$), being also higher at End than at Start ($p < 0.001$). C_L was not different between cycling and running at End or Mid ($p = 0.999$ and $p = 0.966$, respectively), but it was lower during cycling at Start ($p = 0.037$). Adjusting for body mass, there was a significant time effect ($F = 27.668$, $p < 0.001$, $\eta^2_p = 0.634$), as well as a time × modality interaction ($F = 4.248$, $p = 0.023$, $\eta^2_p = 0.21$) for C_L . C_L adjusted for body mass was not different between running and cycling at any time point. Cycling C_L increased from Start to Mid ($p = 0.009$) and then increased further from Mid to End ($p < 0.001$), being significantly greater at End than at Start. Running C_L did not change from Start to Mid, but it was significantly greater at End than at Mid ($p = 0.004$) or Start, with a 3.4 ± 2.5 % increase from Start to End.

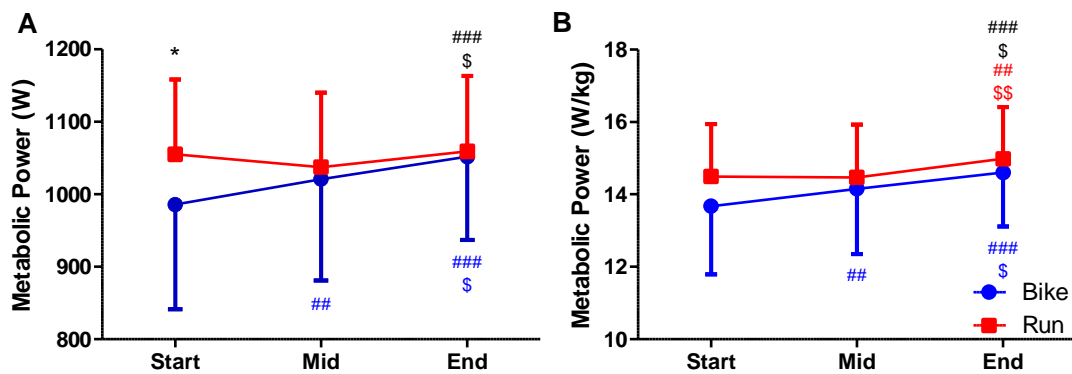


Figure 27. Changes in Cost of locomotion throughout the constant load trials in cycling and running. Panel A shows changes in absolute metabolic power. Panel B shows changes relative to body mass. *, significant difference between modalities at the same time point, $p < 0.005$; ##, significantly different from Start, $p < 0.01$; ###, significantly different from Start, $p < 0.001$; \$, significantly different from Mid $p < 0.05$. Black symbols refer to changes for both modalities together, blue symbols refer to changes in cycling, red symbols refer to changes in running.

Substrate utilization

There was a significant time effect on RER ($F = 34.43$, $p < 0.001$, $\eta^2_p = 0.68$), but no effect of modality or interaction (Figure 28A). RER decreased significantly from Start to Mid ($p = 0.001$) and decreased further from Mid to End ($p < 0.001$). There was a significant effect of time for CHO utilization ($F = 26.88$, $p < 0.001$, $\eta^2_p = 0.63$), with no modality or interaction effects. CHO utilization decreased from Start to Mid ($p = 0.003$) and from Mid to End ($p = 0.002$, Figure 28B).

There was a significant time effect for lipid utilization ($F = 38.87$, $p < 0.001$, $\eta^2_p = 0.71$), as well as a significant time \times modality interaction ($F = 5.49$, $p = 0.009$, $\eta^2_p = 0.26$). Post hoc analysis revealed that lipid utilization increased from Start to Mid ($p = 0.001$) and then to End ($p < 0.001$) during cycling, and it did not increase from Start to Mid ($p = 0.096$), but increased from Start and Mid to End ($p < 0.001$ and $p = 0.04$, respectively). However, there were no significant differences in lipid utilization between modalities at the same time point (Figure 28C).

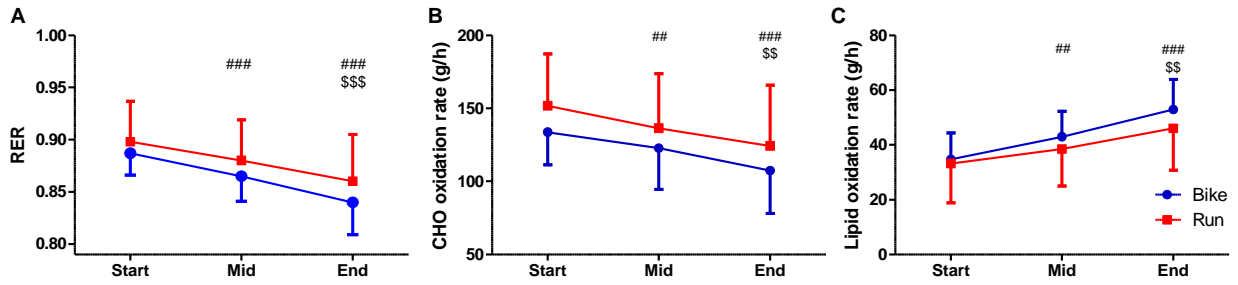


Figure 28. Changes in RER (panel A), carbohydrate (CHO) oxidation rate (panel B) and lipid oxidation rate (panel C) during 3 h of running and cycling. RER, respiratory exchange ratio. There were no differences between modalities. ##, significantly different from Start, $p < 0.01$; ###, significantly different from Start, $p < 0.001$; \$\$, significantly different from Mid, $p < 0.01$; \$\$\$, significantly different from Mid, $p < 0.001$.

Ventilation and heart rate

There were significant effects of modality ($F = 22.81$, $p < 0.001$, $\eta^2_p = 0.56$) and time ($F = 27.73$, $p < 0.001$, $\eta^2_p = 0.634$) on \dot{V}_E but no interaction effects. \dot{V}_E was significantly smaller for cycling than for running ($p < 0.001$, Figure 29A), and it increased throughout the test, from Start to Mid ($p = 0.042$) and then from Start to End and Mid to End ($p < 0.001$ for both).

There were significant modality ($F = 21.50$, $p < 0.001$, $\eta^2_p = 0.573$) and time ($F = 40.611$, $p < 0.001$, $\eta^2_p = 0.717$) effects on HR, (Figure 29B) but no interaction effects. HR was smaller during cycling compared to running ($F = 40.611$, $p < 0.001$, $\eta^2_p = 0.72$). There were no significant increases in HR between Start and Mid ($p = 0.140$) but HR increased significantly from Mid to End ($p < 0.001$).

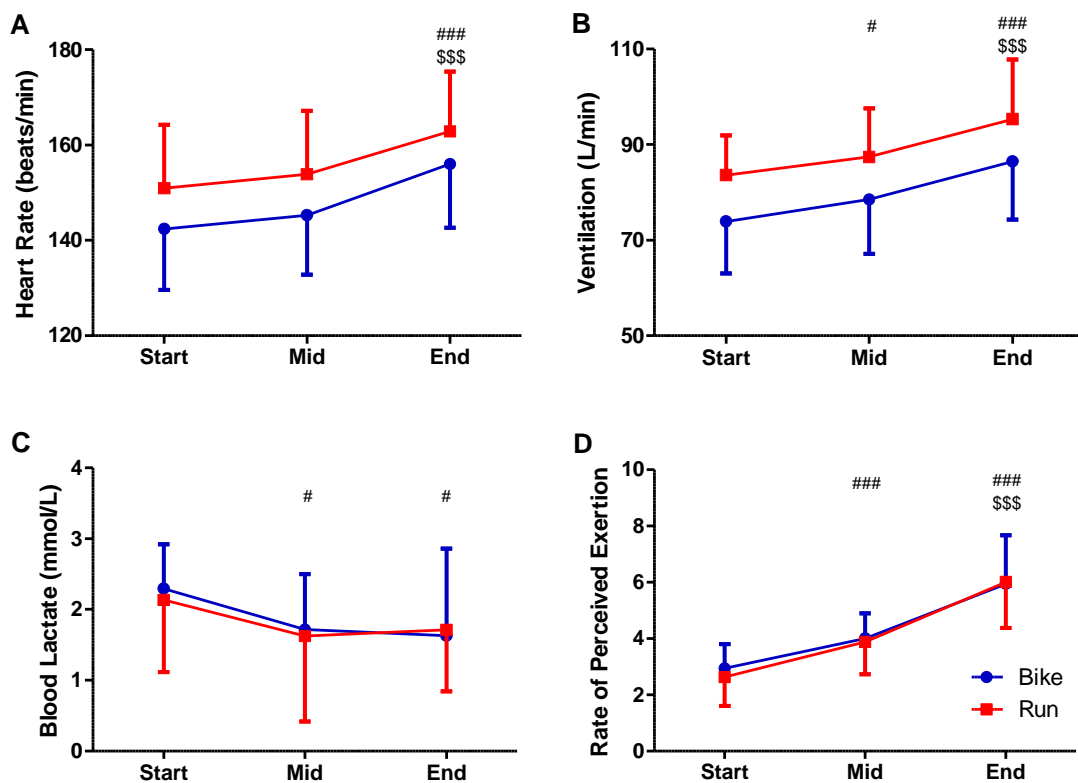


Figure 29. Changes in heart rate (panel A), ventilation (panel B), blood lactate concentration (panel C) and rating of perceived exertion (panel D) during 3 hours of running and cycling. #, significantly different from Start, $p < 0.05$; ###, significantly different from Start, $p < 0.001$; \$\$\$, significantly different from Mid, $p < 0.001$.

Blood Lactate Concentration

There was time effect ($F = 4.86$, $p = 0.014$, $\eta^2_p = 0.23$) for blood lactate concentration, but no effect of modality and no interaction effect. Lactate concentration decreased (Figure 29C) from Start to Mid and End ($p = 0.029$ for both) and it did not change further from Mid to End ($p = 1.000$).

Rate of Perceived Exertion

There was an effect of time ($F = 88.16$, $p < 0.001$, $\eta^2_p = 0.86$) on RPE but no effect of modality and no interaction effect. RPE increased significantly (Figure 29D) from Start to Mid ($p < 0.001$) and then from Mid to End ($p < 0.001$).

Correlations with Fatigue and Cadence

As shown in Figure 30A, there was no significant correlation between the change (Δ) in C_L and ΔMVC (bike: $r = -0.439$, $p = 0.078$; run: $r = 0.241$, $p = 0.35$). There was a significant correlation between ΔC_L and ΔF_0 for cycling ($r = -0.637$, $p = 0.006$) but not for running ($r = 0.115$, $p = 0.659$, Figure 30B).

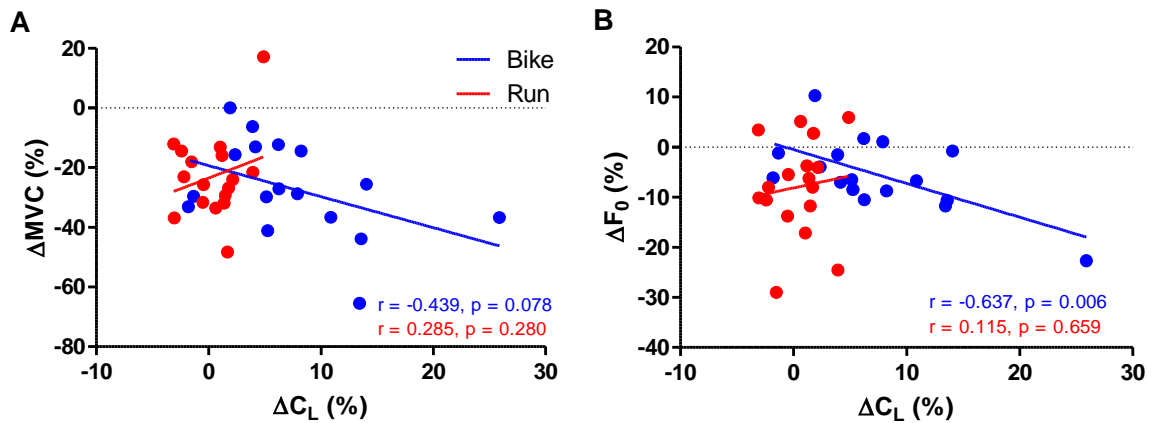


Figure 30. Correlations between changes in cost of locomotion and changes in maximal voluntary contraction of the quadriceps (ΔMVC , panel A), and maximal theoretical force derived from the Force-Velocity profile (ΔF_0 , panel B).

ΔC_L during cycling correlated significantly with Δ cadence at mid-test and at the end of the test (Figure 31). There were no significant correlations between ΔC_L in running and step frequency (r ranging from -0.091 , $p = 0.711$).

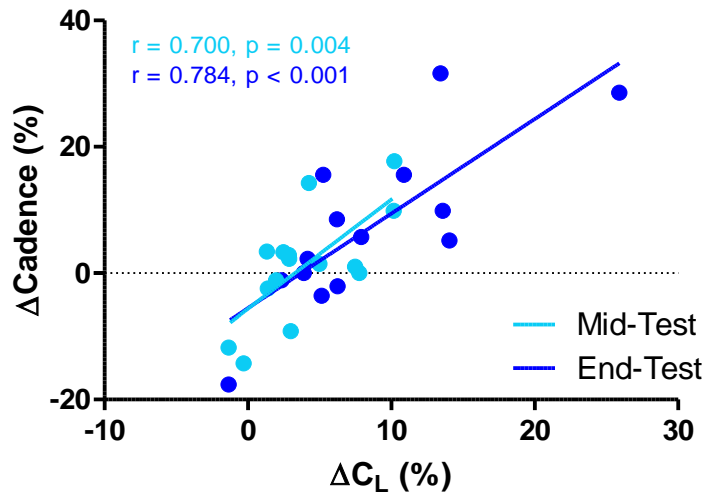


Figure 31. Relationship between changes in cost of locomotion (CL) and cycling cadence, at Mid and End test.

Discussion

The purpose of this study was to compare the effect of running vs cycling on changes in cost of locomotion after prolonged exercise matched for duration and intensity, at 105% of modality-specific GET. Our results showed that running C_L did not change throughout exercise, while cycling C_L increased significantly from the start of the exercise to the mid-point and from then to the end of exercise. The difference between exercise modalities were not caused by changes in cardio-respiratory variables or substrate utilization, since there were no differences in the changes of any of those variables between running and cycling. However, the differences may be related to the development of fatigue, since there was a significant correlation between changes in F_0 and in C_L for cycling.

Maximal exercise tests

No differences were found in terms of $\dot{V}O_{2max}$ between both exercise modalities. However, $\dot{V}O_2$ at GET, absolute and relative to $\dot{V}O_{2max}$ in the same modality, as well as HRmax were lower during cycling. Millet et al. (2009) reviewed the literature that compared physiological parameters measured in running and cycling in athletes that were trained in running, cycling and both modalities (triathletes). Our results are in line with what was found, namely, no differences in $\dot{V}O_{2max}$ between running and cycling when athletes are well trained in both modalities, a significantly higher GET in running compared to cycling and greater HRmax in running compared to cycling.

Changes in cost of locomotion and relationship with fatigue

Running C_L remained constant during the three hours. Although cycling C_L was lower than running C_L at the Start timepoint, it increased significantly during the test, so it was not different than running C_L at Mid and End. To the best of our knowledge, no previous study has reported the responses of C_L during running and cycling exercise of the same duration and metabolic stress (i.e., relative intensity in relation to the GET). Previous research suggests that cycling C_L increases after exercise (Hagan et al., 1992; Hagberg et al., 1978; Hopker et al., 2017; Lepers et al., 2000; Passfield & Doust, 2000) and the response of running C_L has been shown to be variable, and perhaps more dependent on duration and intensity (Gimenez et al., 2013; Sabater Pastor et al., 2021; Xu & Montgomery, 1995). Millet et al. (2000) found an increase in cycling C_L , but not in running C_L after a 65 km running race, which may suggest that cycling C_L may be more sensitive to changes due to previous exercise, independently of the modality of the previous exercise. The differences in changes in C_L in the present study were not related to the differences in any of the physiological variables measured, as they changed in a similar way throughout exercise in both modalities.

When assessing the changes in CL accounting for body mass, greater CL at End was observed for both exercise modalities. This shows that there was an increase in the cost of transporting body mass during running, reflecting a loss in running economy, which was offset by the loss of weight during exercise, leading to no changes in absolute CL. Despite this increase in CL when accounting for body mass, the increase in CL was greater after cycling than after running.

ΔC_L correlated significantly with ΔF_0 , and but the correlation between ΔC_L and ΔMVC in cycling did not reach significance ($p = 0.078$). Furthermore, there was a strong correlation between ΔC_L and $\Delta cadence$ during the test. This suggests that the increase in cadence could be one of the main drivers of the increase in C_L , since the change in cadence explains 61% of the increase in C_L . Previous research has shown that higher cadences result in losses of cycling efficiency (Ettema & Loras, 2009), i.e. a greater C_L , partially explained by the greater cost of rotating the legs more frequently. To explore this further, we tested the correlations between changes in cadence and ΔF_0 and ΔMVC . We found that changes in cycling cadence were significantly correlated to both ΔF_0 and ΔMVC (Figure 32). These combinations of relationships, i.e. (i) ΔC_L vs ΔF_0 , (ii) ΔC_L vs $\Delta cadence$, (iii) $\Delta cadence$ vs ΔF_0 and ΔMVC , suggest that these phenomena are interrelated. The decrease in F_0 following the constant

intensity cycling protocol indicates that force production capacity of the lower limb extensors was impaired. Since the power is fixed, the decrease in force production must be compensated by increasing cadence to sustain power, possibly trying to produce a further loss in force, and this increase in cadence leads to an increase in C_L . Therefore, we speculate that the greater C_L is a consequence of the increased cadence, a strategy used to try to minimize muscle fatigue. In running, there were no relationships between fatigue and changes in C_L . It has been shown that a running fatiguing task induces changes in step length and frequency (Morin et al., 2011; Morin et al., 2011). These changes in running pattern may help the fatiguing muscles to make temporary adjustments that contribute to a smaller loss in economy. However, we did not find relationships between changes in step frequency and changes in C_L and therefore it is not clear what was the main driver of the increase in C_L when accounting for body mass.

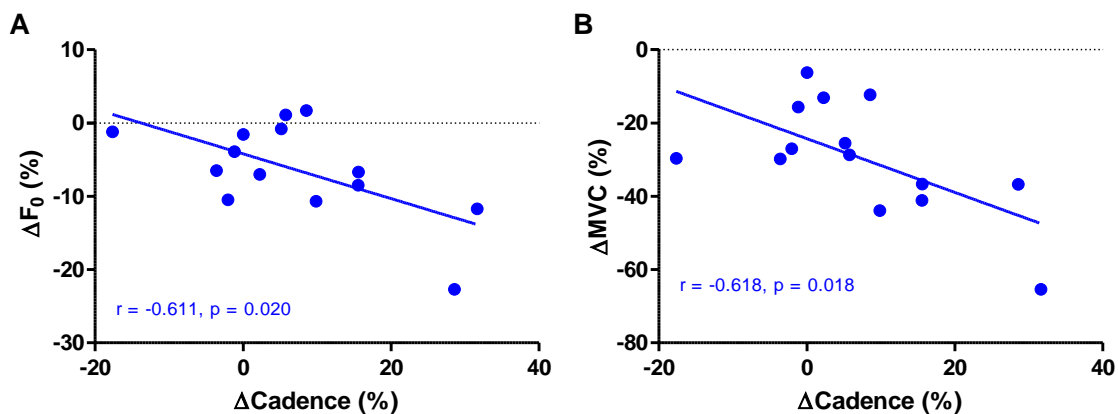


Figure 32. Relationships between changes in cycling cadence and changes in F_0 (panel A) and MVC (panel B) post-cycling exercise.

Physiological and Perceptual Responses to Prolonged Running and Cycling Exercise

As expected, substrate utilization changed during the three hours of exercise in both exercise modalities, with no differences between them. There was a decrease in RER, which is explained by a decrease in CHO oxidation and an increase in lipid oxidation (Péronnet & Massicotte, 1991). The changes in substrate utilization are probably caused by glycogen depletion during exercise, but they cannot explain the differences in cycling C_L , since there were no differences in the changes in substrate utilization during cycling and running. Previous research has shown no differences in changes in RER, CHO and lipid oxidation rates when

comparing running and cycling exercise (Utter et al., 1999) at 75% of $\dot{V}O_2\text{max}$ measured in the same modality.

Whereas \dot{V}_E was significantly lower in cycling at every time point, likely due to the slightly lower intensity relative to $\dot{V}O_2\text{max}$, its rate of increase was not significantly different between exercise modalities. It has been suggested that an increase in \dot{V}_E can contribute to increased C_L , mainly due to the higher energy consumption of the respiratory muscles (Candau et al., 1998). Therefore, it is unlikely that an increased cost of ventilation was the driver of increased energy consumption in our study.

HR was significantly lower at all time points during cycling compared to running, and it did not change significantly from Start to Mid in either modality, but then increased significantly for both modalities from Mid to End. When HR was measured as a percentage of HRmax, it behaved in a similar fashion, but it was not significantly different between modalities at End. This phenomenon, an increase in HR during prolonged endurance exercise, the so-called cardiovascular drift, has been extensively described and seems to be related to dehydration and hyperthermia during exercise, which reduces stroke volume (Coyle & González-Alonso, 2001) in connection to reduced diastolic filling (Dawson et al., 2005). Previous research has shown no differences between the increase in HR between running and cycling at the same intensity in hot temperatures, as well as a similar reduction in stroke volume, despite greater increases in rectal temperature during running (Wingo et al., 2020). Furthermore, the Start-to-End increase in HR correlated with the increase in C_L in cycling, but not in running. However, it is unlikely that the increased energy utilization of the heart causes a significant increase in C_L in one exercise modality and not the other. It is perhaps more likely that the increase in \dot{V}_E and HR are consequences, and not causes, of the increased C_L , since a greater energy demand would require larger ventilation and cardiac output, to provide oxygen to oxidize the energy substrates. However, this would not explain why \dot{V}_E and HR were also increased during running, despite no changes in C_L .

Blood lactate concentration was not different between modalities, and it decreased significantly after the start of exercise. This change may be related to the shift from CHO to lipid utilization to provide energy for exercise, since lactate is a product of CHO metabolism. Previous research found no significant differences in the changes in lactate concentration after 2.5 hours of cycling and running at the similar intensities, which were greater than the exercise intensity prescribed in the present study (Utter et al., 1999).

RPE increased significantly throughout exercise, but in a similar way for both modalities. This is interesting, since it shows that perceived exertion did not increase more during cycling than running, despite an increase in the energy demands of cycling. Contrary to the present results, an effect of modality (running vs cycling) on the increase in RPE during 2.5 hours of exercise has been previously reported, with cycling RPE increasing less than running RPE (Utter et al., 1999).

Limitations

Although not a limitation *per se*, it should be highlighted that the absolute intensity was lower at the start for cycling than for running. The cycling intensity required less metabolic power, as well as a lower $\dot{V}O_2$ and lower percentage of $\dot{V}O_{2max}$ than running. However, a lower intensity would be expected to have a lower impact on the increase in P_{met} , but the effect of cycling on P_{met} was greater than the effect of running.

The intensity of the long-duration trials was selected based on GET, so the required metabolic rate would be sustainable for 3 hours. While all participants reported that the intensity felt easy enough from a cardiovascular perspective to complete the task, some of them had specific issues that prevented them to complete the task at the pre-set intensities. Four athletes had muscle problems, such as cramps, during the first 3-hour test, in three cases during running and in one case during cycling. These problems required a reduction of the intensity by $11.3 \pm 4.5\%$ during an average of 52 ± 39 min. To keep the same intensity and duration during both tests the intensity was decreased during the second test by the same percentage and at the same time-points, so the total duration at a lower intensity was exactly matched. However, one athlete suffered from knee pain while running during the second 3-h test, which forced a 21.3% reduction of running speed during 20 minutes towards the end of the test. Eliminating that participant from our analysis did not change any of the main effects or interaction effects in our results.

As can be seen in Figure 31, one participant had a much greater change in cycling C_L than any other participant. Removing this participant from the analyses resulted in no differences in any of the ANOVA analyses.

Conclusions

Cycling induced an increase in absolute C_L after three hours of exercise at 105% of GET, while C_L remained constant during the three hours of running. Relative to body mass, there was an increase in C_L after both cycling and running, but the increase was still greater after cycling. The greater changes in C_L in cycling were not explained by any of the physiological or perceptual variables assessed, including substrate utilization, heart rate, ventilation, blood lactate concentration, and rate of perceived exertion, since they all changed in a similar fashion for both modalities. Yet, the greater change in C_L in cycling maybe due to fatigue of the locomotor muscles in this modality which resulted in elevated cadence, known to deteriorate efficiency in cycling.

Résumé du Chapitre 4

- Un exercice de course prolongé a un effet négatif sur l'économie de course (RE). Les changements de RE sont fonction de l'intensité et la durée de l'épreuve. Cependant, cela pourrait être moins vrai après un ultramarathon.
- Les mécanismes potentiels qui peuvent affecter les changements de RE après un exercice prolongé incluent la fatigue neuromusculaire, la masse du coureur, les changements biomécaniques, la rigidité des muscles et des tendons, la température, les altérations cardiorespiratoires et les changements dans le métabolisme musculaire.
- L'étude 3 a montré que les courses de trail de moins de 60 km avaient un impact négatif plus important sur RE que les courses de plus de 100 km. Les changements de RE mesurés à plat sont corrélés aux changements mesurés en côte.
- L'étude 4 a montré que les changements du coût de la locomotion étaient plus importants en cyclisme qu'en course à pied lorsque les deux exercices étaient effectués pendant 3 heures à une intensité équivalente. Les changements du coût de la locomotion en cyclisme peuvent être affectés par la fatigue neuromusculaire conduisant à une augmentation de la cadence de pédalage.

5. General discussion and perspectives

The work of this thesis focused on two main aspects: the performance factors of prolonged endurance running (Chapter 3) and the effects of previous prolonged exercise on one of those factors: running economy (Chapter 4). The main findings of this thesis are:

- Elite road and trail runners differ in terms of dynamic maximal power production capacity and maximal strength measured in dynamic conditions, as well as in terms of C_r , with trail runners being more powerful and stronger, while having higher C_r at relatively higher speeds (Study 1).
- Performance in trail running events between 40 and 100 km is mostly influenced by $\dot{V}O_{2max}$. Performance in races between 40-55 km is also predicted by lipid utilisation during moderate intensity exercise, while performance in 100 km races is also predicted by maximal isometric strength and body fat percentage. The factors that predict performance in very long races (> 145 km and 24 h) are still unclear (Study 2).
- C_r increased after trail running events ranging from 40-55 km, but not after events longer than 100 km, whether C_r is measured during flat or uphill running. Furthermore, the changes in flat C_r were correlated with changes in uphill C_r (Study 3).
- C_L increased more after 3 h of cycling exercise than after 3 h of running exercise at matched intensity. Changes in C_L during cycling were related to changes in cadence and neuromuscular fatigue, but the causes of changes of C_r are still unknown (Study 4).

In this section of the manuscript, I will focus on discussing the new results of this thesis and the new questions that are still unknown, some of which have been previously mentioned in the individual discussion of each study.

5.1. Differences between performance factors of road vs trail runners

The work in this thesis is the first to present differences between road and trail runners in some of the variables that may determine performance. Furthermore, it presented these differences in elite athletes, including the world champions in trail running. We showed that elite trail runners were stronger than road runners, when evaluated in dynamic conditions, but they have greater C_r when running at 14 km/h. Since most of the testing was done during

training camps, which meant that there was little time available for testing, since athletes had other activities which were the main focus of the camp, such as training sessions, socializing with the rest of the team and coaches, and sponsor commitments, the amount of testing that we could do was limited. We were required to fit all testing for each athlete in approximately 75 minutes, and it was not possible to do intense physical tests that would leave the athletes fatigued for the rest of their training session. Due to this, we were limited in terms of the variables that we could test for. First, as explained in Study 1, we were limited, due to our equipment, to a maximum treadmill incline of 10%, which may not have been sufficient to show differences in Cr between road and trail runners. Second, we were not able to test maximal aerobic capacity with, for example, an incremental treadmill test to exhaustion, which would have allowed us to determine $\dot{V}O_{2\max}$ as well as metabolic thresholds. A comparison of these variables between road and trail runners is lacking in the literature, and it is probably the next step to assess differences between elite road and trail runners. There is ample literature reporting physiological variables of elite road runners (Daniels & Daniels, 1992; Jones, 2006; Jones et al., 2021; Pollock, 1977). Pollock (1977) tested 20 elite distance runners from the United States, finding an average $\dot{V}O_{2\max}$ of 76.9 ± 3.6 ml/kg/min. Furthermore, the runners were divided in two groups, middle-distance and long-distance track runners (11) and marathon runners (8), with one runner not being classified in any of the two groups. Track runners had higher significantly higher $\dot{V}O_{2\max}$ than marathon runners (78.8 ± 3.2 vs 74.1 ± 2.6 ml/kg/min), while their O_2C was significantly higher than that of marathon runners. Interestingly, the testing included two elite athletes with very similar performances over 5000 and 10000 m: Steve Prefontaine (best times: 13:21.87 min in 5000 m, 27:43.6 in 10000m) and Frank Shorter (best times: 13:26.62 min in 5000 m, 27:45.91 in 10000m, Olympic gold and silver medal winner in the marathon in 1972 and 1976 respectively). Prefontaine's $\dot{V}O_{2\max}$ was measured at 84.4 ml/kg/min, while Shorter's was 71.3 ml/kg/min. Those two values were the highest and lowest $\dot{V}O_{2\max}$ values measured in that study, and they were both measured in the best performing athletes of that sample. In contrast, Shorter showed the lowest values of O_2C (177 ml O_2 /kg/km). This shows that while a relatively high $\dot{V}O_{2\max}$ is a requirement for running success, performance is determined by a combination of factors, and athletes with extraordinary running economy can succeed despite relatively low $\dot{V}O_{2\max}$. Jones et al. (2021) tested 16 world class marathon runners that were pre-selected for the project to run a marathon under 2 h. The mean $\dot{V}O_{2\max}$ in that group was 71.0 ± 5.7 ml/kg/min, with the highest value around 84 ml/kg/min, while the mean O_2C was 189 ± 14 ml/kg/km, with the lowest O_2C measured being ~ 170 ml/kg/min. No studies have taken a similar approach, measuring these physiological

variables in elite trail runners, and therefore very little data is available in the scientific literature. However, there is some data from one of the most successful trail runners of the last decade, Kilian Jornet, multiple times world champion and winner of several high-profile races across a range of distances, including the UTMB, Western States 100, Zegama Aizkorri and Sierre-Zinal. On a report of his acclimatization strategy for his record attempt to the Everest, his $\dot{V}O_2\text{max}$ was reported to be 92 ml/kg/min (Millet & Jornet, 2019). To the best of my knowledge, no other reports of $\dot{V}O_2\text{max}$ values in elite trail runners are available in the scientific literature. The specialized press in trail running has sometimes reported the $\dot{V}O_2\text{max}$ values of some famous athletes. A $\dot{V}O_2\text{max}$ of 90.2 ml/kg/min was reported for Matt Carpenter, record holder of the Pikes Peak Marathon (Eisman, 1998). However, values from the press must be considered carefully, since extraordinary values are more likely to be reported due to them being more newsworthy. One of the subjects tested for Studies 2 and 3 was an elite trail runner, who had previously won and finished on podiums in important races such as the Grand Raid de la Reunion, Hardrock 100 and the UTMB, and his $\dot{V}O_2\text{max}$ was measured at 73.3 ml/kg/min.

Furthermore, during the data collection for Study 1, we also tested some elite female runners, but not enough female road runners were tested to make a comparison. Data on the differences between elite female road vs trail runners is also lacking. Testing of some elite female trail runners in our laboratory has yielded $\dot{V}O_2\text{max}$ values of 66.0 and 70.2 ml/kg/min, while $\dot{V}O_2\text{max}$ values in elite female road runners have been reported to be as high as approximately 80 ml/kg/min in a world record holder in the marathon (Jones, 2006) while average values of 68 ml/kg/min were reported for elite marathon and track long-distance female runners (Daniels & Daniels, 1992). Future research in this area should focus on measuring differences between road and trail runners in a wider set of variables, and possibly using specific performance tests as well (i.e. time trials on the track or during steep uphill and downhill running, walking economy during very steep uphill hiking, local muscular endurance, etc.) Moreover, while uncommon among elite athletes, it is relatively common for recreational and amateur athletes to compete in both modalities, road and trail running. Therefore, to determine the importance of different factors on road vs trail running performance, a correlational study could be conducted, measuring a set of variables in runners who are used to training and competing in both modalities, and then performing two different races or time trials, on the road and the trails, to determine the differences in performance determinants in each modality.

Beyond genetics, training probably is the main factor influencing the determinants of performance in endurance running. Little has been written in the scientific literature about the

training of trail runners. To the best of our knowledge, Study 1 of this thesis presents the first data in the literature on training of elite trail runners, while comparing it with data from elite road runners. We found that trail runners spent only around 55% of the time that elite road runners spend training, and this is despite trail runners in our sample being world class, winners of the World Championships as a team, while road runners were national class runners and therefore at a relatively lower level in their sport. The only other data that we have found in the literature is from the abovementioned study on Kilian Jornet, which reported that his training volume increased from 600 h per year in 2002 as a 15-year-old, to 1,140 h per year in 2017. This higher training volume, equivalent to 95 hours per month, is equivalent to more than double the average in the group of trail runners that we tested, and still 43 monthly hours more than the trail runner who trained most in our sample. This may be partially explained by the fact that trail runners in our group, despite their high level of performance in their sport, were not full-time professional athletes, and had other jobs, while Kilian Jornet is a full-time sponsored professional, and therefore may have more time available to train.

The training volume reported by Jornet is similar or slightly higher than that of successful athletes in other endurance sports such as cross-country skiing (Solli et al., 2017; Tønnessen et al., 2014; Torvik et al., 2021), which usually ranges between 800 and 1,100 hours. In the case of road runners, their time spent training is probably more similar to that reported for other endurance runners (Enoksen et al., 2011), although the training of road and trail runners is often reported in distance run, and therefore an exact comparison is difficult. A relationship between higher running volumes and performance has been shown in runners of different levels, ranging from recreational to elite (Casado et al., 2021; Foster et al., 1977). Furthermore, it has been shown that Kenyan world-class runners performed more training than European-level or National-level Spanish runners and this training difference explained the differences in performance (Casado et al., 2020). Furthermore, Foster et al. (1977) showed that a 20% increase in weekly training volume (15.6 km/week, on average) of recreational marathon runners was associated with a 5% improvement in marathon time (9.9 min on average). Therefore, there is evidence suggesting that higher training volumes are associated with better endurance performance, and it is possible that the elite trail runners in our sample, who perform less training than other elite endurance athletes, may improve their performance by increasing their training volume. However, this may not be possible while trail runners are not able to become full-time professionals, since then they may not have enough time available (to train and, perhaps more importantly, to recover) due to financial reasons. Furthermore, the fact that

trail runners train much less than road runners to achieve the level of world champions, while still being able to keep a full-time job, raises doubts on the “elite” status of trail runners. It has been suggested that the performance level of elite trail runners is lower than that of road runners and other professional endurance athletes such as cyclists or triathletes, who train full-time (Millet, 2012). The lower performance density in trail running contributes to this belief, as Millet reported, the difference between the winner and the 5th finisher in major trail running events was greater (10-19%) than in established endurance sports such as marathon and Ironman triathlon (3-5%). It has been suggested that this may be caused by the fact that trail running is still a young sport, with low economic incentives compared to road running.

Future research could explore the yet unexplored relationship between training volume and other training variables on both performance and physiology of trail runners. Indeed, that was part of the project of my thesis. A project was planned, and started, with the goal of taking an exploratory approach to shed light on this question. At the end of 2019, 31 trail runners were recruited to visit the laboratory four times during a year, to take several physiological measures across the season, including measures of $\dot{V}O_2\text{max}$ and Cr, body composition and isokinetic strength. Athletes then recorded and reported all their training, and completed questionnaires on fatigue, sleep, and overtraining, using a phone application. Furthermore, a second cohort of more than 200 trail runners was recruited to report all of the same data and complete regular performance tests on their own, including a critical speed test (Kordi et al., 2019) and a submaximal running test. The goal was to use that data to perform correlational analyses between different training variables and performance and physiological variables. However, that project was halted due to the Covid-19 pandemic, which led to a national lockdown and the cancelation of trail running races and prevented the subjects from being tested in the laboratory. We had 22 of the 31 runners come back for testing in the laboratory after the national lockdown, which lasted 8 weeks during which outdoor exercise was limited to one hour per day and within a 1 km radius from the home. The trail runners in our sample were able to maintain their, body composition, strength levels and Cr on flat ground, but they had a greater Cr during uphill running at 12% incline, perhaps caused by the lack of access to hilly terrain and mountains in their training. In the larger cohort we saw that training load decreased by 14% during the lockdown due to the shorter duration of the training sessions, and a lower total training duration, despite no changes in intensity and increased training frequency. A study with a similar is currently being planned in our laboratory with the goal of exploring the relationships between training, performance and physiology in trail runners. Further interventional studies

should focus on manipulating training variables to confirm the effect of such manipulations on the physiology and performance of trail runners.

5.2. The role of $\dot{V}O_2\text{max}$ in mountain ultramarathon races.

Previous research has shown that $\dot{V}O_2\text{max}$ is a performance determinant in trail running races of different distances, ranging from XS to XL race categories and 27 to 107 km in duration. However, the previous results in the literature (Coates et al., 2021; Gatterer et al., 2020) as well as the results of study 2 have failed to show a relationship between $\dot{V}O_2\text{max}$ and performance in races that were longer than 120 km, or that approached 24 h for most study subjects. There are several reasons why this could be the case. First, it is possible that $\dot{V}O_2\text{max}$ may not be a relevant performance determinant in mountain ultramarathons of such long distance. Many other factors other than physical fitness influence performance in races of such duration. Due to the length of the races, it is not possible to obtain energy only from endogenous sources, which requires athletes to consume food during the races. However, it is common for athletes in ultra-endurance running events to report gastrointestinal problems (Costa et al., 2016; Stuenkel et al., 2013; Stuenkel & Hoffman, 2015) and therefore it is common that they do not consume enough carbohydrates and protein to meet the current recommendations (Tiller et al., 2019; Wardenaar et al., 2015). Therefore, the ability to tolerate food ingestion and digestion during exercise may be an important factor in ultramarathon performance. Similarly, athletes in races longer than 24 h will suffer from sleep deprivation, and a better ability to tolerate sleep deprivation may be beneficial for performance. Other factors such as pacing, resistance to muscle damage, or better ability to thermoregulate (either physiological ability or better decision making relating to changing clothes during the course) may all be important for performance. Therefore, if there are many other factors that may influence performance in long-distance ultramarathon racing, it is logically necessary that the relative importance of physiological factors such as $\dot{V}O_2\text{max}$ must be lower. An athlete with a very high $\dot{V}O_2\text{max}$ may be beaten in a race by an athlete with much lower aerobic capacity, if the first one makes tactical mistakes regarding hydration, nutrition and layering, because those mistakes can lead them to issues such as dehydration, hypoglycemia, heat stroke or hypothermia, which may force them to slow down their pace, take rest stops and even abandon the competition.

Despite the previous issues, data collected in our laboratory for another study completed in the UTMB in 2009 shows that a relationship between $\dot{V}O_2\text{max}$ and performance in mountain ultramarathons longer than 24 h probably still exists. In that study, some of the results from

which have been published by our group (Martin et al., 2010; Millet et al., 2011; Morin et al., 2011), 34 male trail runners participating in the UTMB were tested prior to the race, and 22 of them were able to complete the race (average time = 37.5 ± 5.9 h). The greater number of finishers led to a more normal distribution of performances than in Study 2. Significant correlations were found between race time and several variables, including $\dot{V}O_2\text{max}$ ($r = -0.724$, $p < 0.001$, Figure 33), peak speed during the incremental treadmill test ($r = -0.823$, $p < 0.001$), $\dot{V}O_2$ relative to $\dot{V}O_2\text{max}$ at the anaerobic threshold ($r = -0.510$, $p = 0.018$), body fat percentage ($r = 0.527$, $p = 0.012$), and O_2C ($r = 0.493$, $p = 0.020$).

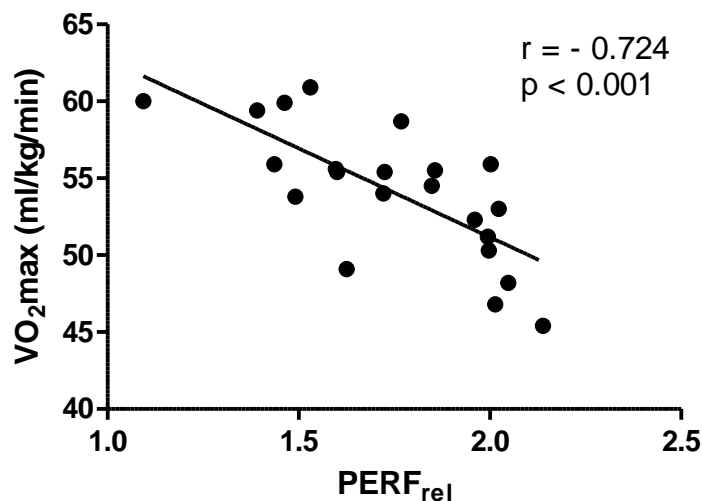


Figure 33. Relationship between performance relative to the winner ($PERF_{rel}$, performance relative to the winner expressed as Performance Time / Winner's Time) and $\dot{V}O_2\text{max}$ in the UTMB 2009 study.

The data from the 2009 UTMB study suggests that physiological variables, especially those related to maximal aerobic capacity, are still important in trail running races longer than 24 hours. Perhaps the way in which performance variables such as aerobic capacity, running economy, anthropometry or muscle strength and power affect performance in mountain ultramarathon races is not as straightforward as it is in road races or races of shorter distance. A better way to approach the influence of physiological factors of performance in ultramarathon may be to consider them to be not determinants of performance, but rather limiting factors. For example, $\dot{V}O_2\text{max}$ or the LTP limit the highest sustainable speed in a competition. Therefore, having high $\dot{V}O_2\text{max}$ and LTP values is necessary, but not sufficient, for performance in this type of events. However, since other factors such as resistance to muscle damage, sleep management, decision making and the ability to ingest food and drink during exercise also limit performance in this type of events, it is possible that working on improving the classic

performance factors of endurance running may not yield improvements in performance if, for example, a runner with an already high $\dot{V}O_2\text{max}$ is limited by their inability to digest CHO during exercise.

5.3. Assessment of Cr: treadmill and road vs specific assessment on trail

One issue with the assessment of Cr is that all the research to date on the importance of Cr as a performance factor in trail running has used assessments of Cr on a treadmill (Balducci, Cl  men  on, et al., 2017; Ehrstr  m et al., 2018; Scheer, Janssen, et al., 2019). Some studies have tried to make the assessment of Cr more specific by testing it on an inclined treadmill. It has also been suggested that testing of other variables such as $\dot{V}O_2\text{max}$ and the thresholds at an incline may be more relevant for trail runners, due to the greater specificity (Balducci et al., 2016; Scheer, Janssen, et al., 2019). However, in the discussion of Study 2 we raised another issue related to the testing of Cr as a performance factor in trail running: the specificity of the terrain in terms of ground technicality. In the sport of trail running the amount of energy that is spent to cover a certain distance is probably influenced by two main factors. First, the “physiological” Cr, that is, the energy that the active muscles and other organs must consume to cover a certain distance, which is influenced by the variables detailed in Chapter 3. Second, there is a decision-making component, normally talked about in terms of “technical ability”. To the best of my knowledge, this aspect has not been studied in the scientific literature, but it may be influenced by several factors, including: coordination, the ability to make good decisions when choosing a line or foot placement, the ability to execute properly that decision, so the foot is placed on the intended place, the ability to change direction quickly, using the minimum required amount of force when climbing over obstacles so there is no unnecessary vertical displacement of the center of mass, appropriate decision making on when to transition between running and walking, etc. One study has shown that despite no differences in O_2C during running on a flat, level path experienced orienteers had better O_2C during running on a technically difficult trail than track runners (Jensen et al., 1999), suggesting that the better technical ability of the orienteers allowed them to use less oxygen than the track runners. O_2C was higher for both groups when running on the trail, but it increased significantly more for the track runners.

Furthermore, other tactical decisions of the runner will influence his Cr during the race, such as equipment choices, since lighter equipment will require less energy to carry, and water and food carried between aid stations. For example, an optimal strategy for carrying water would be, in theory, to add just enough water to the bottles so the runner runs out of water just

before the next aid station, and no extra water weight is ever carried during a race. Yet another tactical aspect to take into account is that these tactical decisions often involve trade-offs, for example sometimes runners may make a decision that could increase Cr while decreasing muscle damage, such as using hiking poles or wearing heavier, more cushioned shoes, as suggested by Millet et al. (2012). These aspects may interplay with each other, sometimes magnifying their effects. For example, runners who are confident in their technical ability may choose to wear lighter shoes, providing less cushion and protection, and stronger runners may choose not to use hiking poles in some courses saving the weight and trusting their strength will protect them from muscle damage, and those strategies would also decrease Cr. These are all reasons why Cr measured on a treadmill may not be a good predictor of trail running performance.

During my PhD studies, I collaborated with another project, investigating the effect of trail technicity on Cr and biomechanics (Nicot et al., 2021, appendix 3). The data that we collected supports the idea that RE measured on a treadmill may be not be relevant for trail runners. A group of 10 runners was tested while running uphill on two different trails of 1 km in length and 200 m of elevation gain. The elevation gain was measured for every 100 m segment, and each trail was simulated on a treadmill test of 1 km, in which each 100 m section was matched for incline with the average incline of each 100 m section of the corresponding trail. Therefore, each runner performed two tests on two different trails and two tests on the treadmill, while RE was measured using a portable metabolic cart. Figure 34 shows the Cr data from those 10 athletes. There was a significant correlation between Cr in both trail running segments ($r = 0.680$, $p = 0.031$), and a significant correlation between Cr in both treadmill tests ($r = 0.689$, $p = 0.028$). However, there was no significant correlation between Cr in each trail and Cr in its corresponding treadmill test ($r = 0.146$, $p = 0.688$ and $r = 0.396$, $p = 0.257$).

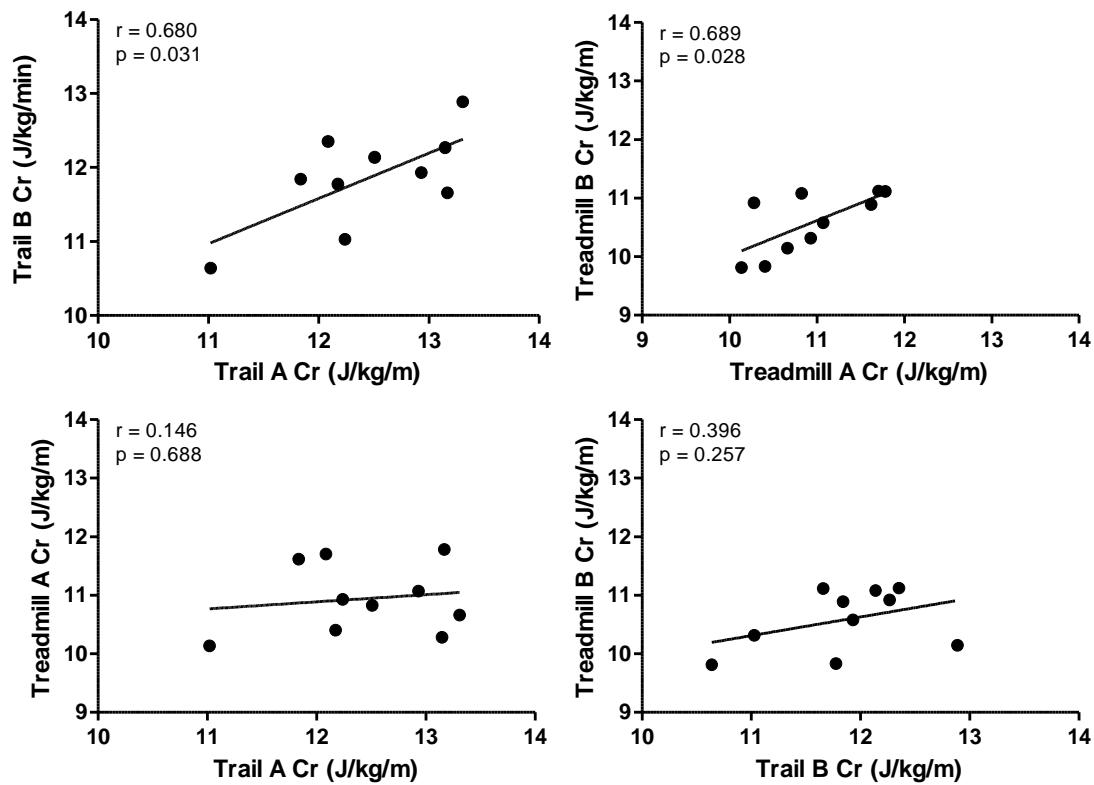


Figure 34. Relationship between Cr measured in two different trails (top left) two different treadmill uphill tests (top right) and between Cr measured in each trail and its corresponding treadmill test (bottom left and right).

While these data must be interpreted carefully, considering the small sample size and the fact that the experiment was not designed to establish this lack of relationship between RE measured on treadmill and on trail, the data suggests that it is possible that Cr during trail running may not be as strongly related to Cr during treadmill running as previously assumed. Therefore, two goals are proposed for future research in this area:

1. Establish the relationship, or lack thereof, between Cr measured on technical terrain and measured on a treadmill. For this, a similar design to the study in appendix 3 may be suitable, with a group of runners performing tests in two different trails and two different tests on treadmill, perhaps adding another condition, measuring economy on two different roads. Examining the correlation between the two tests in the same type of condition and the correlations between different conditions would let us know if RE on trail is actually unrelated to RE on a treadmill.

2. If a lack of relationship is shown, further research should focus on establishing what are the factors that influence RE on trail. While it is likely that RE measured on a treadmill will still be one of the factors that influence RE on trail, the influence of other factors such as coordination, experience, balance, and perceptual and decision-making skills may influence RE on trail. Elucidating the importance of these factors may allow practitioners to develop training plans to improve these individual factors, therefore improving Cr during trail running.
3. It must be considered that it is possible that previous trail running exercise may have a different effect on Cr measured on a treadmill vs Cr measured on a trail, since the fatiguing running exercise may also have a negative effect on coordination or the ability to choose the optimal path or the most appropriate foot placements. If the goal of the post-exercise assessment is to find out the possible amount of impairment that Cr has suffered by the end of the race, testing should be done in terrain similar to that of the race.

5.4. Changes in Cr after ultramarathon running: can running economy really improve?

Study 3 was the first one in the literature directly testing the effect of distance on changes in Cr, suggesting that changes in Cr after prolonged running exercise occur after short duration races, but they may not occur after ultramarathon races. Evidence collected after ultramarathon races has shown that it is even possible that Cr may decrease after mountain ultramarathon running. However, only two studies have shown decrements in Cr after ultramarathon running (Vernillo et al., 2014, 2016), and those two studies are very particular for two reasons: first, the race in which those studies were conducted was the Tor des Geants, a 330 km race with 24,000 m of elevation gain. This is an extremely long distance, much longer than the most popular ultramarathon races, which are around the 100 miles distance (~160 km). Therefore, extrapolating the fact that Cr decreased after Tor des Geants to state that Cr “decreases after ultramarathons” may not be adequate, since Cr in other ultramarathon races and tests, ranging from 43 km to 24 h on a treadmill, have shown either no changes or increases in Cr (Vernillo, Millet, et al., 2017). Second, the three measurements that showed a lower Cr after ultramarathon running in both studies by Vernillo et al. (2014, 2016) were performed during uphill running, and one measurement that was performed during flat running (Vernillo et al., 2014) did not show significant changes in Cr. Therefore, it is possible that ultramarathon running does not decrease Cr in general, but it may only have a positive effect on uphill Cr. In

Study 3, we found that there was a good correlation between flat and uphill Cr and, moreover, a strong correlation between changes in flat Cr and uphill Cr (Figure 26). However, the changes in uphill Cr were relatively smaller than the changes in flat Cr (by 2.54 percent points on average, although not significantly different), and the variability in the changes was greater during flat (range -12 to +31%) than during uphill running (range -7 to +20%). This suggests the possibility that uphill Cr is may be sensitive to increases after an ultramarathon. Most importantly, it suggests that, despite the significant correlation between changes in flat and uphill Cr, they may be different measures which must be considered separately. A further example of the interaction between ultramarathon distance and slope is the study by Vernillo et al. (2015) in which athletes were tested after a 65 km mountain ultramarathon. They found significant increases in Cr during flat and downhill running, with the increase being greater for flat running, while a non-significant increase was reported for Cr during uphill running. All these data are in line with the results of Study 3, which showed that Cr increased significantly after races shorter than 60 km, but not after races longer than 100 km. Therefore, it is possible that the distance of the race and the slope of the treadmill during the test both affect changes in Cr after trail running races. It is possible that Cr increases after shorter ultramarathon races (< ~60 km), while it may not change following races in the 100 – 170 km range, and Cr may decrease after races beyond 300 km. Furthermore, it is possible that flat and uphill Cr are influenced by some independent factors, meaning that they are two different constructs that must be measured separately. Future research should aim to clarify this question, using consistent methods regarding the slope at which Cr is tested before and after mountain ultramarathon races of different distances, to determine if there is a true decrease in Cr after mountain ultramarathons, and what is the distance at which a decrease in Cr may be expected.

5.5. Causes of changes in Cr after prolonged running exercise

The causes of changes in Cr after prolonged running exercise are not known. Previous research has shown that greater intensity for the same duration of exercise is more detrimental for Cr than lower intensity (Xu & Montgomery, 1995), and that greater duration for the same sustained intensity is also more detrimental (Brueckner et al., 1991). This suggests that duration and intensity interact to impair Cr. In Study 3 we found that Cr was impaired after races <60 km, but not after races >100 km, and we speculated that the greater intensity during the shorter races may be responsible for this difference. In the case of trail running, the greater intensity may have an especially important impact during downhill running, leading to greater muscle damage and inflammation, which may cause greater fatigue and pain, and possibly affect Cr

negatively. Furthermore, speeds and impact forces are higher during testing of Cr on the flat, and this may be one of the causes of the greater impairments in Cr during flat running compared to uphill running. The greater speed and impact may induce more pain in the muscles, which could have a harmful effect for Cr, for example forcing athletes to change their running pattern, decreasing stride length and therefore increasing frequency. No data have been published showing a direct relationship between those changes in running pattern and Cr, and there was no relationship between changes in stride frequency and changes in Cr after 3 h of running in Study 4, it is theoretically possible that an increase in stride frequency could lead to increases in Cr, since the internal cost of moving the legs would be increased. Furthermore, uphill running relies more on concentric contractions of the leg muscles, while flat running relies more on the stretch-shortening cycle. It is possible that the mechanisms of the stretch-shortening cycle may be more negatively affected than the capacity to produce force during concentric contractions by prolonged running, especially including downhill running, therefore leading to greater impairments in Cr during flat than during UH running. Another reason why Cr during uphill running may be differently affected than flat Cr may not be the slope itself, but the speed. Uphill running requires slower speeds, and it is possible that the faster speed during flat, requiring for example a greater contribution of the stretch-shortening cycle, is partly responsible for the greater detriment in Cr measured during flat running.

As previously explained in section 4.2., there are several physiological mechanisms that may have an impact in changes in Cr after prolonged running exercise, including neuromuscular fatigue, temperature, carried mass, biochemical and metabolic changes, muscle and tendon stiffness and changes in running biomechanics. However, the impact of each of these mechanisms on changes of Cr after prolonged running is not known. To the best of my knowledge, there is no published data that shows that any of these mechanisms is responsible for changes in Cr. Using the data from Study 3, together with the other data published by our laboratory from the same race (Besson et al., 2021; Espeit et al., 2021; Koral et al., 2021; Temesi et al., 2021), we assessed the correlations between changes in Cr and changes in neuromuscular fatigue. No relationships were found between changes in either flat or uphill Cr and changes in maximal voluntary contraction or changes in F_0 or v_0 obtained from the force-velocity profile test, suggesting that changes in neuromuscular fatigue are not related to changes in Cr after prolonged trail running races. We also assessed the relationship between changes in Cr and blood markers of muscle damage (creatine phosphate kinase) and inflammation (C-reactive protein) collected for another study on the same athletes and at the same event (Robert et al.,

2020; Skinner et al., 2021), and no relationships were found between any of these blood markers and changes in Cr, even when splitting the results by race distance. In Study 4, we assessed the relationships between changes in Cr and neuromuscular fatigue after 3 h of treadmill running and no relationship was found. We also assessed the correlation between changes in Cr and changes in several biomechanical variables, including step frequency, contact time, flight time and vertical and leg stiffness, and no correlations were found between any of the biomechanical variables and changes in Cr. This suggests that neuromuscular and biomechanical changes or muscle damage may not be the main factors affecting changes in Cr after prolonged running.

Future research should focus on trying to elucidate what are the mechanism that lead to increases in Cr after prolonged running exercise and the interventions that might help mitigate the effect of those mechanisms on Cr. Furthermore, research should aim to identify the causes of the different responses of Cr measured during uphill and flat running, and if they are related to the more concentric nature of uphill running.

5.6. Changes in cost of cycling after prolonged cycling exercise

In Study 4 we compared the consequences on C_L of two prolonged exercise at the same intensity in two common exercise modalities: running and cycling. This allowed us to test the effect of exercise with different type of contraction on C_L , since the stretch-shortening cycle is prevalent in running, while contractions are mostly concentric during running. Furthermore, we assessed the differences in neuromuscular fatigue induced by each exercise modality (Brownstein et al., under review). We found a greater increase of C_L during cycling than during running. Similar to running, the main factors that influence cost C_L during cycling are not well understood. A review by Ettema and Loras (2009) found that there are two main factors that affect cycling efficiency: absolute power output and cadence. They found that power output is the main determinant of gross efficiency, with greater power outputs resulting in greater efficiencies. They suggested that this likely occurs due to the fact that at greater power outputs a lower percentage of the metabolic power consumed is used to spin the legs, and a greater percentage of the metabolic power is used transferred to the pedals. They also found that power output explained 91% of the variance in metabolic cost. They also found a negative relationship between efficiency and cadence, meaning that greater cadences require more metabolic energy. Adding cadence to the model increased the explained variance to 94%, with cadence on its own explaining about 10% of the variance. However, a problem of the previous research is that power output and cadence have been included at the same time as independent variables in the

experiments. Since the effect of power output is so strong, it is very difficult to discern what are the variables that affect C_L when power is held constant, and what are the variables that may change during prolonged cycling exercise that may be responsible for the changes in C_L . In our study, with power held constant, we found a strong correlation between the increase in cycling cadence and the increase in metabolic power (Figure 32, Chapter 4), with changes in cadence explaining 61% of the variance in changes of C_L at the end of the 3 h. Furthermore, there was a significant negative correlation between changes in F_0 from the force-velocity profile and changes in C_L , and a non-significant correlation between changes in MVC and changes in C_L (Figure 30, chapter 4). These correlations suggest that neuromuscular fatigue may be related to the changes in the C_L . Therefore, we also assessed the relationships between changes in cadence and changes in F_0 or changes in MVC, and we found significant negative correlations (Figure 32, chapter 4), suggesting that fatigue is related to the changes in cadence. However, the direction of causality is not clear. It is possible that fatiguing muscles are less capable of producing force, and therefore subjects may be required to increase their cadence to sustain the fixed power output. Otherwise, it is also possible that the greater force production required to sustain a lower cadence may be more fatiguing than lowering the force production per pedal stroke while increasing the cadence. Therefore, it is possible that cyclists modify their cadence when their fatigue trading off an increase in C_L to decrease muscle fatigue, in a similar fashion of what has been suggested may happen in ultramarathons (Millet et al., 2012). Further research should focus on understanding the changes in C_r when cadence is fixed, as well as the different fatiguing effect of pedaling at different cadences but sustaining the same power output.

5.7. Effect of prolonged running on other performance factors

Chapter 4 of this thesis focused on the assessment of C_L after prolonged endurance exercise, aiming to quantify changes in C_L after competitive trail running events and after controlled exercise in laboratory conditions. Maunder et al. (2021) proposed the concept of durability as an important concept to define in athlete profiling, and they defined durability as “the time of onset and magnitude of deterioration in physiological-profiling characteristics over time during prolonged exercise” and they suggested that “understanding ‘durability’ at the level of the individual athlete may allow more specific intensity regulation during long-duration training sessions, training load monitoring and programming, and prediction of exercise performance.” The assessment of the changes in variables beyond C_L after prolonged exercise may indeed be helpful. Beyond differences at the individual level, it may be interesting to investigate the effect of these variables that different exercise modalities have, such as cycling

vs running, or the effect of running at different inclines. Furthermore, we suggested that one of the drivers of greater changes in Cr following trail running races <60 km compared to races >100 km may be the greater intensity during the shorter races. Therefore, testing the effect of different exercise intensities on the magnitude of deterioration of these variables may also be important.

Some recent research has shown that critical power, a measure of the second threshold related to fractional utilization, is impaired after prolonged cycling exercise. Clark and colleagues performed a series of studies on the effect of previous exercise in the heavy intensity domain on critical power, the boundary between the heavy and the severe intensity domain (Clark et al., 2018; Clark, Vanhatalo, Thompson, Joseph, et al., 2019; Clark, Vanhatalo, Thompson, Wylie, et al., 2019). They showed that the power at the end of a 3-min all out test, which is a measure of critical power (Vanhatalo et al., 2007) was decreased after two hours of exercise in the heavy intensity domain (Clark et al., 2018). The same group then replicated the result that the magnitude of change in critical power was not correlated to changes in muscle glycogen (Clark, Vanhatalo, Thompson, Wylie, et al., 2019), but critical power did not change if CHO were ingesting during the 2 h fatiguing task, and it was not reduced after only 40 or 80 min (Clark, Vanhatalo, Thompson, Joseph, et al., 2019). Furthermore, time to exhaustion in the heavy domain was lower than expected, showing that the fractional utilization was decreased for a given duration. This research by Clark and colleagues suggests that threshold parameters are also sensitive to changes after fatiguing exercise, and that the magnitude of changes may be duration-dependent when the intensity is fixed.

It seems that the effect of previous exercise on $\dot{V}O_{2max}$ has not been extensively researched, despite $\dot{V}O_{2max}$ being perhaps the most studied parameter in exercise physiology and one of the main predictors of endurance performance. $\dot{V}O_{2max}$ during incremental exercise did not change after 6 min at 90% of the power at $\dot{V}O_{2max}$ in a previous test followed by 6 min of rest (Marles et al., 2006) or in the second incremental test performed 30 min after a previous incremental test (Caillaud et al., 1996). However, we are not aware of any research that has measured the effect of prolonged exercise on $\dot{V}O_{2max}$. This seems relevant, since the fraction of $\dot{V}O_{2max}$ that can be sustained seems to be an important factor in endurance performance. If $\dot{V}O_{2max}$ decreases during exercise, it would mean that a greater fraction of $\dot{V}O_{2max}$ must be sustained to keep the same exercise intensity. Equally, in sports which may require high intensity efforts at the end of a race, such as cycling or track running, an impairment in $\dot{V}O_{2max}$ caused by the previous exercise could limit the maximal output of the athlete for that final effort.

Future research should study the effect of previous exercise on other variables beyond $\dot{V}O_{2\max}$, considering the effects of different types of exercise, such as different exercise intensities, durations and modalities. Indeed, some preliminary data from Study 4, in which an incremental test was also performed after the 3 h trials, shows that there was no effect on cycling $\dot{V}O_{2\max}$ (-1.9%, $p = 0.099$), while there was significant reduction in maximal power achieved during the test (-8.15%, $p < 0.03$). The reduction of $\dot{V}O_{2\max}$ in running was greater than in cycling ($-8.1 \pm 8.0\%$ vs $-1.9 \pm 9.1\%$, $p = 0.006$), but there were no differences in the reduction of maximal intensity achieved ($-9.9 \pm 7.2\%$ in cycling vs $-12.7 \pm 6.8\%$ in running). This data from Study 4, together with data from other studies recently performed in our laboratory, may help shed some light on the effects of previous exercise on $\dot{V}O_{2\max}$ and the variables that correlate with, and may explain, those changes. This evaluation of performance factors after fatiguing tasks is necessary to have a global understanding of fatigue. The traditional evaluation of fatigability has consisted in neuromuscular testing, taking measures of maximal voluntary contraction, and using different types of electrical or magnetic stimulation. This type of evaluation gives insights into the neural and muscular mechanisms of fatigue responsible for a decrease in maximal strength. However, the decrease in maximal strength may not be the most relevant consequence of fatiguing tasks in sport or daily life. For example, in the case of endurance running or cycling it is theoretically possible to have a decrease in MVC without an impairment in performance, since the force required to perform the task is much lower than the MVC. Similarly, MVC may not change while performance is deteriorated. Therefore, it seems important to investigate the consequences of fatiguing exercise on other variables such as $\dot{V}O_{2\max}$, fractional utilization, and Cr, to obtain a holistic understating of the impact of fatiguing exercise on performance.

Resumé du Chapitre 5

- Nous avons fourni les premières données sur les différences entre les coureurs sur route et les coureurs de trail élite pour certains facteurs de performance. Cependant, les différences au niveau d'autres facteurs de performance, comme la $\dot{V}O_2\text{max}$, sont encore inconnues.
- Le rôle de la $\dot{V}O_2\text{max}$ dans la performance en ultramarathon n'est pas clair. Nous n'avons pas montré de relation entre la $\dot{V}O_2\text{max}$ et la performance dans l'étude 2. Cependant, d'autres données suggèrent que le $\dot{V}O_2\text{max}$ peut encore être pertinent pour la performance en ultramarathon. Il est possible qu'une $\dot{V}O_2\text{max}$ plus élevée soit bénéfique pour la performance en ultramarathon, mais son importance pourrait être moindre que pour les distances plus courtes, en raison de nombreuses autres variables influençant la performance en ultramarathon.
- Il est possible que l'évaluation de RE sur un tapis roulant ne soit pas représentative de RE sur les sentiers, puisque d'autres facteurs tels qu'une meilleure coordination ou la prise de décision pourraient influencer l'économie de course sur les sentiers.
- Il est également possible que la distance de la course et l'inclinaison du tapis roulant pendant le test affectent les changements de l'économie de course après les courses d'ultramarathon. Les recherches futures devraient viser à évaluer l'effet de la pente lors du test sur les changements d'économie de course après les ultramarathons.
- Plusieurs causes pourraient influencer les changements du coût de la locomotion après un exercice prolongé de course et de cyclisme. En cyclisme, la cadence et la fatigue semblent contribuer aux changements du coût de la locomotion.
- D'autres facteurs tels que les seuils métaboliques et la $\dot{V}O_2\text{max}$ peuvent changer après un exercice d'endurance prolongé. L'évaluation des changements dans ces variables devrait faire partie d'une évaluation complète de la fatigue après un exercice d'endurance.

6. Conclusion

The work of this thesis aimed to fill gaps in the literature regarding the performance determinants of trail running and the consequences of prolonged exercise on Cr. Previous to this thesis, there was no knowledge about what are the potential differences in terms of performance determinants between elite road and trail runners. Furthermore, the effect of race distance on the importance of different factors that influence trail running was not known. The work contained in this thesis demonstrated that elite road and trail runners differ in terms of maximal power production capacity and strength, as well as in terms of Cr, with trail runners being stronger and more powerful but less economical at higher running speeds. This thesis has also furthered the understanding of performance factors in trail running races, showing that aerobic capacity is the main correlate of performance in races up to 100 km, and that performance in races < 60 km is also influenced by substrate utilization, while performance in 100 km races is also influenced by maximal strength and body composition.

Regarding changes in C_L following prolonged endurance exercise, the research suggested the possibility that Cr could remain stable, or even decrease, after mountain ultramarathon races, which was unexpected considering the increase in Cr following endurance running exercise of shorter duration. Furthermore, the impact of different exercise modalities, which involve different types of muscle contractions, on Cr was not known. This work has also shown that Cr is impaired by trail running races < 60 km, but not by races > 100 km. Finally, this thesis has provided the first insight into the changes on C_L induced by two different modalities of exercise matched for intensity and duration, cycling and running, showing that cycling induced greater changes in C_L than running. It is proposed that future investigations should further seek to further our understanding of these topics, including (i) the determinants of performance in road vs trail running and in trail running races longer than approximately 145 km and 24 h, (ii) the relevance of testing RE in specific terrain as a performance predictor of trail running, as well as to assess the changes in RE on specific terrain after prolonged running, (iii) the causes and mechanisms leading to changes in C_L after prolonged endurance exercise, and (iv) the changes in other performance factors induced by prolonged exercise.

Conclusion (Français)

Cette thèse visait à combler certaines des lacunes de la littérature concernant les déterminants de la performance de la course de trail et les conséquences d'un exercice prolongé sur la fatigue. Avant cette thèse, il n'existait aucune connaissance sur les différences potentielles en termes de déterminants de la performance entre les coureurs élités sur route et les coureurs élite de trail. De plus, l'effet de la distance de course sur l'importance des différents facteurs qui influencent la course de trail n'était pas complètement connu. Le travail de cette thèse a démontré que les coureurs d'élite sur route et de trail diffèrent en termes de capacité de production de puissance maximale et de force, ainsi qu'en termes d'économie de course, les coureurs de trail étant plus forts et plus puissants mais moins économes à des vitesses de course plus élevées. Cette thèse a également permis de mieux comprendre les facteurs de performance dans les courses de trail running, en montrant que la capacité aérobie est le principal corrélât de la performance dans les courses jusqu'à 100 km, et que la performance dans les courses < 60 km est également influencée par le type de substrats oxydés, tandis que la performance dans les courses de 100 km est également influencée par la force maximale et la composition corporelle.

En ce qui concerne les changements du coût de la locomotion après un exercice d'endurance prolongé, il a été suggéré la possibilité qu'il reste stable, voire diminue, après des courses d'ultramarathon en montagne, ce qui était inattendu compte tenu de l'augmentation de RE après un exercice de course d'endurance de plus courte durée. En outre, l'impact des différentes modalités d'exercice, qui impliquent différents types de contractions musculaires, sur le coût de la locomotion n'était pas connu. Mon travail a montré que RE est altérée par les courses de trail < 60 km, mais pas par les courses > 100 km. Enfin, cette thèse a fourni le premier aperçu des changements sur le coût de la locomotion induits par deux modalités différentes d'exercice appariées en intensité et en durée, le cyclisme et la course à pied, montrant que le cyclisme induit des changements plus importants que la course à pied. Il est proposé que les recherches futures visent à approfondir notre compréhension de ces sujets, y compris (i) les déterminants de la performance dans la course sur route par rapport à la course de trail et pour des courses de trail d'une durée supérieure à environ 145 km/24 h, (ii) la pertinence de tester RE sur un terrain spécifique trail en tant que prédicteur de performance en course de trail, (iii) investiguer les causes et les mécanismes conduisant à des changements du coût de la locomotion après un exercice d'endurance prolongé, et (iv) étudier les changements induits par un exercice d'endurance prolongé sur des facteurs de performance autres que RE.

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List of publications and communications

Scientific Articles

Sabater Pastor F., Varesco G., Besson T., Koral J., Feasson L., Millet G.Y. (2021) Degradation of energy cost with fatigue induced by trail running: effect of distance. *European Journal of Applied Physiology*. 121(6), 1665-1675.

Sabater Pastor F., Besson T., Berthet M., Varesco G., Kennouche D., Dandrieux P.E., Rossi J., Millet G.Y. Neuromuscular characteristics and economy of elite road vs trail runners. *Under review in Journal of Strength and Conditioning Research*.

Sabater Pastor, F., Besson, T., Varesco, G., Parent, A., Fanget, M., Koral, J., Foschia, C., Rupp, T., Rimaud, D., Féasson, L., Millet, G.Y. Physiological determinants of performance in trail and ultra-trail running races of different distances. *Under review in International Journal of Sport Physiology and Performance*.

Sabater Pastor, F., Faricier, R., Metra, M., Murias, J. M., Brownstein, C. G., Millet, G. Y. Changes in cost of locomotion after endurance running vs cycling exercise matched for intensity and duration. *To be submitted*.

Nicot, F., **Sabater Pastor, F.**, Samozino, P., Millet, G.Y., Rupp, T. (2021) Effect of ground technicity on cardio-respiratory and biomechanical parameters in uphill trail running. *Accepted in European Journal of Sport Science*.

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Besson T., Parent A., Brownstein C.G., Espeit L., Lapole T., Martin V., Royer N., Rimaud D., **Sabater Pastor F.**, Singh B., Varesco G., Rossi J., Temesi J., Millet G.Y. (2021). Sex

differences in neuromuscular fatigue and changes in cost of running after mountain trail races of various distances. *Medicine and Science in Sports and Exercise*. 53(11), 2374-2378.

Congress Communications

ORAL | **Sabater Pastor F**, Besson T, Varesco G, Parent A, Fanget M, Koral J, Foschia C, Rupp T, Rimaud D, Féasson L, Millet GY. (2021). Physiological determinants of performance in trail running races of different distances. *26th annual congress of the European College of Sport Science (Online)*.

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ORAL | **Sabater Pastor F**, Besson T., Berthet M., Varesco G., Kennouche D., Rossi J., Millet G.Y. Physiological Differences between Elite Male Trail vs Road Runners. *18th congress of the Association des Chercheurs en Activités Physiques et Sportives, 28-31 Oct 2019, Paris (France)*.

Appendices

Appendix 1. Cost of running, biomechanical and neuromuscular characteristics of elite vs experienced male and female trail runners

This is a summary of a paper written by Thibault Besson and is part of his thesis work. This work was conducted in parallel to Study 1.

Author list: Thibault Besson, **Frederic Sabater Pastor**, Giorgio Varesco, Marilyne Berthet, Djahid Kennouche, Pierre-Eddy Dandrieux, Jeremy Rossi, Guillaume Y Millet.

Introduction:

In just over 20 years, trail running (TR) has moved from a niche sport to a major outdoor activity. Flagship races have emerged and more and more good runners belong to teams and get contracts with sponsoring brands. In recent years, international competitions have been organized (European and World Championships) which probably raises the level of the best TR athletes.

One specificity of trail running is that it requires the runners to constantly adapt to external factors such as type of terrain, elevation change, altitude, temperature, etc. TR races generally alternate between uphill and downhill sections that respectively involve a more predominant concentric and eccentric muscle actions compared to classic road races using repeated stretch-shortening cycles. The influence of this type of training on trail runners' neuromuscular function is not known.

Cost of running (Cr) has traditionally been presented as one of the main predictive variables of running performance. Cr measured on uphill incline was reported to be a better predictor of performance than level Cr confirming the specificity of TR compared to 'classic' endurance road running. Since lower limb strength and power have also been suggested to be determinant in TR performance, it would be interesting to analyze how the Power-Torque-Velocity profile (PTVP) of trail runners could potentially discriminate between elite and non-elite.

The aim of this study was thus to compare Cr, neuromuscular function and biomechanical characteristics in elite vs non-elite trail runners and in males vs females. Given the factors of performance in TR described above, the main hypotheses are that (i) elite trail runners will have a better Cr compared to experienced trail runners, especially when measured in uphill condition, and (ii) elites will show greater lower limb muscle strength and power but less velocity capacities compared to experienced trail runners. Regarding sex comparisons, it was hypothesized that (i) no sex differences will be found in Cr, but females will have (ii) shorter contact time, (iii) lower power capacities associated with a less velocity-oriented profile compared to males

Methods:

Forty-one runners, i.e. 21 experienced (EXP, 10F) and 20 elite (ELITE, 10 F) trail runners participated in the study. According to ITRA, runners were considered as elite if, at the time of the test, they had an ITRA performance index of more than 700 for females and up to 825 for males. Runners of the EXP group were asked to (i) have at least one trail race objective in the season, (ii) train at least 3 times/week for the past 12 months and (iii) train for trail competitions.

Neuromuscular performance was assessed in two modalities: during dynamic muscle contractions with a PTVP test, measured using a two-sprint test on a cycle ergometer; and isometric strength was assessed by measuring isometric maximum voluntary contraction (IMVC) of the knee extensors (KE), knee flexors (KF) and hip extensors (HE).

Athletes ran at 10 and 14 km/h at 0% slope (10FLAT and 14FLAT, respectively), and at 10 km/h on a 10% slope on a treadmill (10UH). During each condition, running kinematics were measured and gas exchange data were collected to calculate Cr. Athletes also reported their training during the previous year.

Data are reported as mean \pm SD. A two-factor sex (Males-Females) \times level of performance (EXP-ELITE) factorial ANOVA test was performed.

Results:

Compared to EXP, ELITE were significantly lighter ($p = 0.003$), had a lower body mass index (BMI) ($p < 0.001$), and higher ITRA performance index (PI) ($p < 0.001$) and training volume ($p = 0.006$). Compared to males, females were significantly lighter, shorter, had a lower BMI and lower ITRA PI (all $p < 0.001$).

ELITE had a lower Cr compared to EXP for 10FLAT ($p = 0.029$), 14FLAT ($p = 0.012$) and 10UH ($p = 0.005$) conditions. No main sex effects were observed in Cr for any of the three running conditions.

At 14FLAT, ELITE displayed lower step frequency ($p = 0.035$) and lower limb vertical ($p < 0.014$) and leg ($p = 0.006$) stiffness compared to EXP. In all running conditions, females demonstrated shorter contact times ($p \leq 0.007$), greater step frequency ($p \leq 0.006$) than males. Females also exhibited lower stiffness values than males at 14FLAT ($p \leq 0.006$).

When expressing values relative to body mass, KE maximal strength appeared significantly greater in ELITE ($p = 0.049$) whereas KF maximal strength was greater in EXP ($p = 0.008$). HE values were not significantly different between EXP and ELITE. Males were stronger than females when torque was normalized to body mass for KE ($p = 0.007$) and KF ($p = 0.018$), but there were no sex differences in HE ($p = 0.166$).

In the PTVP, despite no level of performance difference on maximal power (P_{max}) ($p = 0.059$), ELITE showed greater relative T_0 (theoretical maximal torque) ($p = 0.001$) a lower V_0 (theoretical maximal velocity) ($p = 0.002$) and a steeper slope ($p < 0.001$) of the PTVP compared to EXP. Males showed greater T_0 , V_0 and P_{max} values than females ($p \leq 0.009$).

Discussion:

The aim of this study was to compare cost of running, biomechanical and neuromuscular characteristics of experienced and elite trail male and female runners. When examining the effect of the level of performance, the main findings were that (i) compared to EXP, ELITE had a lower (i.e. better) Cr in both level and uphill running, greater lower limb extensors strength capacities (in both isometric and dynamic conditions) but less KF isometric strength, (ii) ELITE displayed a more force and less velocity oriented PTVP compared to EXP. Regarding sex comparisons, the main results are that (iii) females displayed shorter contact times but have similar Cr whatever the slope or speed, and (iv) males and females exhibited a similar slope of the PTVP despite males exhibiting greater power, force and velocity capacities compared to females.

Interestingly, the present study showed that elite trail runners presented a better Cr compared to EXP, and that this was true for both flat and uphill running. Although the present analyses do not permit to assert that Cr is directly linked to TR performance, it seems that a gap exists between the Cr values of experienced trail runners and international elite trail runners,

despite the fact that Cr was measured at relatively low speed which may have minimized the differences between EXP and ELITE.

In trail runners, a recent study from our group reported no differences in Cr between males and females of similar level of performance measured before trail and ultra-trail running races in both flat and uphill conditions. With reporting no sex difference in Cr, the present study is in accordance with these previous findings.

No differences were found between EXP and ELITE in step frequency at 10FLAT and 10UH but this variable was found to be higher in EXP for the 14FLAT condition. This result may be due to the fact that spatiotemporal parameters were measured at absolute running speeds and EXP probably had to differently adjust their biomechanics (i.e. increasing their step frequency) to maintain a higher percentage of their maximal speed at 14 km/h than ELITE. Greater leg and vertical stiffness observed in EXP compared to ELITE at 14 km/h is potentially linked to greater relative muscle activation in EXP, because of higher relative speed, that is known to be positively related to active muscle stiffness.

Similar to the EXP vs ELITE comparison, higher relative speed in females might explain part of the sex differences in spatiotemporal parameters (i.e. greater step frequency and shorter contact times in females compared to males). Despite shorter contact times, females demonstrated both, lower leg and vertical stiffness compared to males at 14 km/h. This could be attributed to sex differences in muscle-tendon unit mechanical properties, i.e. with females presenting more compliant musculo-tendinous properties of the lower limbs.

Interestingly, the present study showed that, independently of the sex, ELITE displayed greater KE IMVC and greater T_0 compared to EXP when expressed relatively to body mass. It could be speculated that ELITE accrued higher elevation gain and training volume, which requires the contribution of lower limb extensor muscles to a greater extent compared to EXP. The maximal power was not different between ELITE and EXP. The explanation is likely related to the fact that the greater T_0 in ELITE was counterbalanced by a greater V_0 in EXP. Greater proportion of slow twitch fibers in ELITE either genetically determined and/or due to greater training volume could potentially explain lower V_0 compared to EXP.

More strength and greater functional performance in males are most probably linked to greater lower extremity muscle mass and a larger cross-sectional area of type II muscle fibres in males compared to females. This could also explain greater V_0 consequently involving greater Pmax in males. The present study also adds novel interesting insight on the PTVP with

observing a similar mechanical profile of male and female trail runners (i.e. no sex difference in the slope of the PTVP).

Conclusion:

The present study showed that, independently of the sex, top world class trail runners have a better cost of running, and different neuromuscular (greater lower limb extensor strength capacities, steeper slope of the torque-velocity relationship) and biomechanical characteristics (lower limb stiffness) compared to experienced trail runners. Independently of the level of performance, similar force-velocity profile was observed between female trail runners despite male reporting more strength, velocity and power capabilities of the lower limb compared to female trail runners. Sex differences were also observed in running biomechanics with females showing shorter contact time, higher step frequency and lower limb stiffness compared to males. However, sex specificities in running biomechanics do not seem to influence the cost of running since no sex differences were observed. Overall, this study brings original data on physiological, neuromuscular and biomechanical characteristics of male and female trail runners of different levels of performance. We suggest that these evaluations should be implemented in the field to help coaches optimizing training in trail running.

Appendix 2. Sex Differences in Neuromuscular Fatigue and Changes in Cost of Running after Mountain Trail Races of Various Distances

Sex Differences in Neuromuscular Fatigue and Changes in Cost of Running after Mountain Trail Races of Various Distances

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²Department of Biological Sciences, Université du Québec à Montréal (UQAM), Montreal, Quebec, CANADA; ³Université Clermont Auvergne, AME2P, Clermont-Ferrand, FRANCE; ⁴Institut Universitaire de France (IUF), FRANCE; and ⁵Faculty of Health and Life Sciences, Northumbria University, Newcastle Upon Tyne, UNITED KINGDOM

ABSTRACT

BESSON, T., A. PARENT, C. G. BROWNSTEIN, L. ESPEIT, T. LAPOLE, V. MARTIN, N. ROYER, D. RIMAUD, F. SABATER PASTOR, B. SINGH, G. VARESCO, J. ROSSI, J. TEMESI, and G. Y. MILLET. Sex Differences in Neuromuscular Fatigue and Changes in Cost of Running after Mountain Trail Races of Various Distances. *Med. Sci. Sports Exerc.*, Vol. 53, No. 11, pp. 2374–2387, 2021. **Introduction:** Women have been shown to experience less neuromuscular fatigue than men in knee extensors (KE) and less peripheral fatigue in plantar flexors (PF) after ultratrail running, but it is unknown if these differences exist for shorter trail running races and whether this may impact running economy. The purpose of this study was to characterize sex differences in fatigability over a range of running distances and to examine possible differences in the posttrace alteration of the cost of running (Cr). **Methods:** Eighteen pairs of men and women were matched by performance after completing different races ranging from 40 to 171 km, divided into SHORT versus LONG races (<60 and >100 km, respectively). Neuromuscular function and Cr were tested before and after each race. Neuromuscular function was evaluated on both KE and PF with voluntary and evoked contractions using electrical nerve (KE and PF) and transcranial magnetic (KE) stimulation. Oxygen uptake, respiratory exchange ratio, and ventilation were measured on a treadmill and used to calculate Cr. **Results:** Compared with men, women displayed a smaller decrease in maximal strength in KE (–36% vs –27%, respectively, $P < 0.01$), independent of race distance. In SHORT only, women displayed less peripheral fatigue in PF compared with men (Δ peak twitch: –10% vs –24%, respectively, $P < 0.05$). Cr increased similarly in men and women. **Conclusions:** Women experience less neuromuscular fatigue than men after both “classic” and “extreme” prolonged running exercises but this does not impact the degradation of the energy Cr. **Key Words:** ENERGY COST, FATIGABILITY, FEMALES, MALES, TRAIL RUNNING

In recent years, participation in trail and ultratrail (defined by the International Trail Running Association as trail races with a distance >80 km) running has increased considerably, with reports of numerous events having to limit registration numbers due to overdemand. However, participation in trail and ultratrail events remains considerably more popular in men than women. For instance, at the UTMB® 2019, one of the most popular ultratrail events in the world, only 257 of

2543 starters, that is, 10%, were women. Despite the low participation rates for women, ultratrail running is one of the rare disciplines in which women have outperformed men in some events (1).

The increasing enthusiasm for trail running has led scientists and researchers to take a particular interest in the physiological and neuromuscular (NM) consequences of prolonged trail running events. Neuromuscular fatigue, also known as performance fatigability, can be defined as the progressive change that occurs in the central nervous system and/or muscles due to exercise, resulting in a force output that is less than anticipated for a given voluntary contraction or stimulation (2). It has been reported from isometric studies in isolated muscle groups that women are less fatigable than men, particularly at submaximal intensities (3). Although part of the sex difference in fatigability has been attributed to greater strength and consequent higher blood flow occlusion in men, previous studies have demonstrated that the sex difference in fatigability during submaximal isometric contractions persists when men and women were matched for strength (4,5). Furthermore, Ansdell et al. (6) assessed sex differences in fatigability relative to

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Appendix 3. Effect of ground technicity on cardio-respiratory and biomechanical parameters in uphill trail running.

This paper, led by François Nicot, was done in parallel during the work of my thesis. It has recently been accepted for publication in the European Journal of Sport Science

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ABSTRACT

The goal of this study was to analyze the effects of ground technicity on cardio-respiratory and biomechanical responses during uphill running. Ten experienced male trail-runners ran ~ 10.5 min at racing pace on two trails with different (high and low) a priori technicity levels. These two runs were replicated (same slope, velocity, and distance) indoor on a motor-driven treadmill. Oxygen uptake, minute ventilation (\dot{V}_E), heart rate as well as step frequency and medio-lateral feet accelerations (i.e. objective indices of uneven terrain running patterns adjustments) were continuously measured throughout all sessions. Rating of perceived exertion (RPE) and perceived technicity were assessed at the end of each bout. Oxygen cost of running (O_2Cr) (+10.5%; $p < 0.001$), \dot{V}_E (+21%; $p < 0.004$) and the range and variability of feet medio-lateral accelerations (+116% and +134%, respectively; $p < 0.001$), were significantly greater when running on trail compared to treadmill, regardless of the a priori technicity level. Despite perceived technicity being lower on treadmill ($p < 0.001$), RPE was not different between trail and treadmill runs ($p < 0.68$). It is concluded that running uphill on a trail vs. a treadmill significantly elevates both O_2Cr and magnitude/variability of feet medio-lateral accelerations but no difference could be identified between trails of different a priori technicities. These results strengthen the need for trainers and race organizers to consider terrain technicity per se as a challenging cardio-respiratory and biomechanical component in uphill trail running.

KEY WORDS: *energy cost of running; uneven terrain; gradient locomotion; feet accelerometry; rating of perceived exertion.*

1. INTRODUCTION

Trail running has exploded in popularity over the past 20 years (Hoffman et al., 2010). Compared with road races, trail running takes place within an unpredictable and multidimensional environment that imposes behavioral and physiological adaptations. The nature of the ground (e.g. smooth or stiff, slippery), slope, total elevation changes, altitude, weather, and sometimes the presence of snow are factors that lead the runners to adapt their running pattern which may have direct neuro-muscular consequences (short-term and long-term fatigue, muscle intracellular disturbances) and increase energy demand.

Positive slopes strongly influence energy demand when running and walking in such environments (Margaria, 1938; Cavagna et al., 1964; Cavagna and Kanero, 1977; Di Prampero et al., 1986; Roberts and Belliveau, 2005). In particular, energy cost linearly increases with the positive slope (Minetti and Saibene, 1992; Minetti, 1995; Minetti et al., 2002). For example, Minetti et al. (2002) showed that the cost of running (respectively walking) grows from 3.40 J/Kg/m (respectively 1.64 J/Kg/m) on flat to 18.93 J/Kg/m (respectively 17.33 J/Kg/m) on a slope of 40%. From a biomechanical point of view, it has been ascertained that running uphill is associated with a reduction in flight time and an increase in stride frequency (SF) (for a review, see Vernillo et al., 2017).

Ground technicity is partly determined by the microrelief made up of materials located at the ground surface (Voloshina and Ferris, 2015). Some of those materials are usually natural parts of the soil. The soil can be consolidated or smooth, and made up of small and/or big asperities. For instance, obstacles can be found on the ground surface, such as plant roots or rocky blocks. Their size, distribution and spacing strongly affect ground technicity that can also be described at surface roughness. However, ground technicity encompasses other aspect of running technical challenge such as whether or not the trail is slippery, if it is dry or wet, etc. As a result, the word technicity will be used in this manuscript. Increasing ground technicity may increase the metabolic demand, as shown in level walking (Voloshina et al., 2013) and level running (Andlof et al., 1976; Jensen et al., 1999; Müller and Blickhan, 2010; Voloshina and Ferris, 2015; Gantz and Derrick, 2018). A granular soil (sand or mud for example) modifies the locomotion. The foot penetrates more deeply within the soil; an important part of the mechanical energy during the foot strike is used to compact the soil and create locally a firm surface able to resist against the load and make the propulsion possible (Lejeune et al., 1998). In addition, the granular nature of the soil reduces the frictional adherence between shoes soles and soil surface, and thus (according to the Coulomb's friction law) reduces the maximal

tangential force that can be generated during the impulsion phase. It turns out that the locomotion is modified from a biomechanical point of view. For instance, a decrease in step length allows to limit the inclination (and thus, the tangential component) of the ground reaction force (Lejeune et al., 1998). The nature of the ground (uneven terrain) may also disturb running patterns throughout two mechanisms. First, the obstacles can be regarded as micro elevations. Even though this elevation is not detectable from common altimetry sensors (such as GPS devices) due to the small amplitude in the oscillations of the body's center of mass, these oscillations could be large enough to increase energy demand (Voloshina and Ferris, 2015). While most of the previous studies focused on the effect of ground technicity on level running, the case of uphill running remains to be investigated. Second, a granular soil or an uneven terrain can lead to modifications in the running pattern and the trajectory with lateral deviations. Indeed, the runner takes care to have a stance as stable as possible. For that purpose, she/he tries to find the best place to put the foot on the ground, which forces her/him to perform foot lateral displacement, and to adjust the step length (and so step frequency) from one step to another. This may also increase energy demand.

While the energy requirements can reasonably be estimated for most track and road events, this is far from being true for trail running races. So far, the difficulty of a trail is assessed mainly through distance and elevation. For example, the International Trail Running Association (ITRA) scale uses the concept of km-effort: $(\text{Distance in km}) + (\text{Vertical gain in m}/100)$. However, despite ground technicity being one of the parameters that strongly determines the difficulty of a trail (see above), it remains poorly investigated (Zamparo *et al.*, 1992; Voloshina and Ferris, 2015; Gantz and Derrick, 2018). For instance, even though the Echappée Belle (263 km-effort with 11400 m of positive elevation) is shorter than the Ultra Trail du Mont Blanc (UTMB, 271 km-effort with 10000 m of positive elevation), the winners' race times are on average 35% longer than those of UTMB. Thus, the technicity of the terrain, which is recognized to be very demanding in the Echappée Belle, is probably a key factor that governs running speed and perceived exertion.

This study aims at testing the effect of ground technicity related to the terrain microrelief on uphill running biomechanics, metabolic demand and perceived exertion. We hypothesized that uneven terrain will increase lateral foot displacements and variabilities in runner's biomechanical pattern, possibly affecting the variability of both SF and foot lateral acceleration. We also hypothesized that ground technicity will increase metabolic demand and perceived exertion.

2. MATERIALS AND METHODS

2.1 General setting

Three visits, separated by at least 48 hours were carried out. Visits 1 and 2 were randomly performed on the terrain on two trails of similar length, slope and total ascent but with different technicity levels, as evaluated subjectively by two trail running experts. They were carried out only under dry weather conditions, in order to ensure the same ground conditions for all the subjects. Visit 3 was performed in the lab and consisted in replicating slope and speed of both trails on a treadmill for the subjects to perform matched runs excluding the technicity component. As the treadmill was assumed to correspond to a reference zero technicity level, the comparison between terrain and treadmill tests allowed determining the specific effect of ground technicity for each trail. During visit 3, runs performed in visits 1 and 2 were reproduced in the same order as on the terrain, with 20 minutes of recovery between the two bouts.

2.2 Subjects

Ten male trail runners [age: 35.4 ± 7.5 years, mass: 69.6 ± 8.2 kg, resting heart rate (HR_{rest}): 49.7 ± 8.7 bpm] were recruited in the local running community to take part in the study. The participants were healthy, and injury free during the previous 6 months. They were chosen to be homogenous with respect to the training level (6 ± 2 hours of training per week) and the experience level (at least 5 years of trail running, including a minimum of 2 competitions yearly). They were also all familiarized with treadmill running. They were asked not to participate in any competition the week before the test and to do only usual, low intensity training during the 3 days before the test. HR_{rest} was recorded every day for 7 days before the test, following the same protocol: in bed, once waked up, just before standing up. Estimated maximal heart rate (HR_{max}) was calculated from the following empirical relations: $HR_{max} = 220 - \text{age}$, if $\text{age} < 42$ and $HR_{max} = 208 - 0.7 \times \text{age}$ otherwise (Tanaka et al. 2001) and was used to define heart rate reserve (HR reserve) to calibrate warmup intensity.

This study complies with the Declaration of Helsinki and has been approved by the local ethics committee. Clearance for participation in the study was granted by written informed

consent after having received full information describing and explaining the study procedures in detail.

2.3 Experimental design

The two selected trails were located along the Eastern side of Montagne-du-Chat, above Bourget-du-Lac campus (Savoie, France) (see Fig. A, supplemental material). The distance of both trails was ~ 1 km. High technicity (HT) trail, that was considered as more technical because of the presence of multiple (roots and rocks) obstacles along the trail, had a global elevation of 200 m between the starting point (alt. 520 m) and the arrival point (alt. 720 m). Low technicity (LT) trail, that was evaluated as less technical, had a global elevation of 190 m between the starting point (alt. 760 m) and the arrival point (alt. 850 m). Furthermore, quasi-constant slopes were preferred to avoid abrupt metabolic adjustments associated with abrupt changes in oxygen uptake ($\dot{V}O_2$) or heart rate (HR), and to rapidly reach a quasi-steady metabolic state. The details on the two trail profiles are available in Table A (supplemental material). Each field test (i.e. LT and HT) started with a standardized 5 min warm-up consisting in running along a flat path at 50% of the HR reserve (Karvonen and Vuorimaa, 1988). The warm-up was followed by 5 min of rest. The subjects were instructed to run at a speed corresponding to the speed they would adopt on the same hill if it was part of a 40 km trail race competition. Immediately after the test (uphill arrival point), each subject reported rating of perceived exertion (RPE) and perceived technicity. Elevation and velocity, as well as weather conditions (temperature and humidity level) were continuously recorded during the test.

HT and LT trails were then simulated in the lab (respectively, Sim-HT and Sim-LT) on a motorized treadmill (Medic Eval ECG2855, Matsport, Ecole-Valentin, France) which was programmed every 100 m for speed and inclination with increments of 0.1 km/h and 0.5%, respectively. In other words, the subjects ran each section of 100 m length at the same average velocity and slope they ran that section in the field. The two simulated bouts were randomly performed on the treadmill at a temperature that reproduced as closely as possible the field conditions by manipulating the air-conditioning system within the lab room. After a standardized 5-min warm-up consisting in flat running on the treadmill (at 50% of HR reserve), followed by 5 min of rest, the first test was carried out. After 20 min of passive recovery, the second test was performed. The same parameters as those during the field tests (see below)

were recorded during the two lab tests. At the end of each bout (Sim-HT and Sim-LT), the subjects were asked to answer the two questionnaires (RPE and perceived technicality).

2.4 Data collection

During each test, the subjects were equipped with a GPS (SUUNTO Spartan Sport, Vantaa, Finland) watch connected to a HR monitor, to record both elevation and velocity at a frequency of 1 Hz. Respiratory exchanges were measured breath-by-breath with an open flow portable metabolic analyzer (K4b2, COSMED, Rome, Italy). Running pattern was investigated with two tri-axial wireless accelerometers (AgileFox, Hikob, Villeurbanne, France) firmly fixed by straps on the top of both shoes above the metatarsals. Accelerations in the three axes were continuously recorded at a sampling frequency of 1,344 Hz which was assumed to be high enough to detect foot-ground contact (peak of the vertical-axis acceleration signal). The accelerometers of both feet were time-synchronized. Finally, after each running bout, subjects had to report the rating of perceived exertion (RPE) using the standard 6-20 Borg scale (Borg, 1970) and the rating of perceived technicality using a 0-10 visual analog scale ranging from 0 (no technicality) to 10 (maximal level of technicality conceivable by the subject). Subjects were free to figure out the technicality level of each trail, as no specific information were given on that.

2.5 Data analysis

2.5.1 Respiratory alterations and energy cost of running

Ventilation (\dot{V}_E , L/min), breathing frequency (br/min), $\dot{V}O_2$ (mL/min/kg) CO_2 production ($\dot{V}CO_2$) and HR (bpm) were continuously measured during all running bouts. Respiratory exchange ratio (RER), ventilatory equivalents ($\dot{V}_E/\dot{V}O_2$ and $\dot{V}_E/\dot{V}CO_2$), and oxygen cost of running (O_2Cr , mL/kg/km) were calculated. The caloric energy cost (kJ/kg/km) will not be considered in this manuscript, as the assessment of the energy equivalent of O_2 (J/mL) derived from the RER (Peronnet and Massicotte, 1991) can be inaccurate when RER exceeds the unity. In addition, as not all the subjects reached a metabolic steady state, considering the caloric energy cost could lead to a wrong estimate of the energy consumption. The data corresponding to the first 20% of each exercise bout was discarded to avoid the steep increase in $\dot{V}O_2$ corresponding to the fast component of $\dot{V}O_2$. The last 20% of each bout was also discarded, because some of the subjects tended to increase exercise intensity at the end of each bout (end-spurt). Therefore, only the period between 20-80% of the duration of each

exercise bout, during which $\dot{V}O_2$ was relatively stable, was considered to explore the running-induced respiratory and metabolic adaptations depending on trail technicity. Signals were filtered using a 5 breath-to-breath cycle moving average (Fig. 1A).

2.5.2 Biomechanical parameters

The feet acceleration signals were filtered using a low-pass, second-order Butterworth filter (cutoff frequency: 5 Hz) and synchronized between the two feet. From the acceleration signal on the foot vertical (z) axis, peak metatarsals accelerations were detected on right and left foot representing the foot-ground contacts. From the latter, step frequency (SF) and inter-step variability in SF (SFsd) were computed from the duration of each step which corresponds to the time interval between successive ground-foot impacts (Fig. 1B). It is worth noting that the overall medio-lateral acceleration level of the foot was quantified by the range of the acceleration signal given by the difference between the maximal and minimal values. As the distribution of these differences is highly non-uniform over the whole-time range considered, the average of this distribution (Fig. 3a) can be much smaller than a particular value as shown in Fig. 1. The time-window of the acceleration signal considered in Figs. 1b and 1c has been randomly selected to illustrate the signal analysis procedure, and corresponds to values greater than the average.

During each stride, the overall medio-lateral movement of each foot was supposed to be associated to the level of acceleration of the foot in the medio-lateral (y) direction. However, it must be acknowledged that relative movements between shoe and bone segments during prolonged running may occur. As no anatomical calibrations were performed to ensure that accelerations are measured with respect to reliable axes in each runner, the top surface of a shoe might not be parallel to the ground during each test. Keeping this limitation in mind, the overall medio-lateral acceleration level of the foot was quantified during each step (determined as previously explained) by the range of acceleration in an approximated M-L axis of the foot, characterizing the recurrent adaptations in the M-L foot position when running. Average (ML) and standard-deviation (MLsd) values were then computed over all steps between 20-80% of the duration of each exercise bout to give some insights about the level of acceleration of the foot in the medio-lateral direction and its inter-step variability respectively.

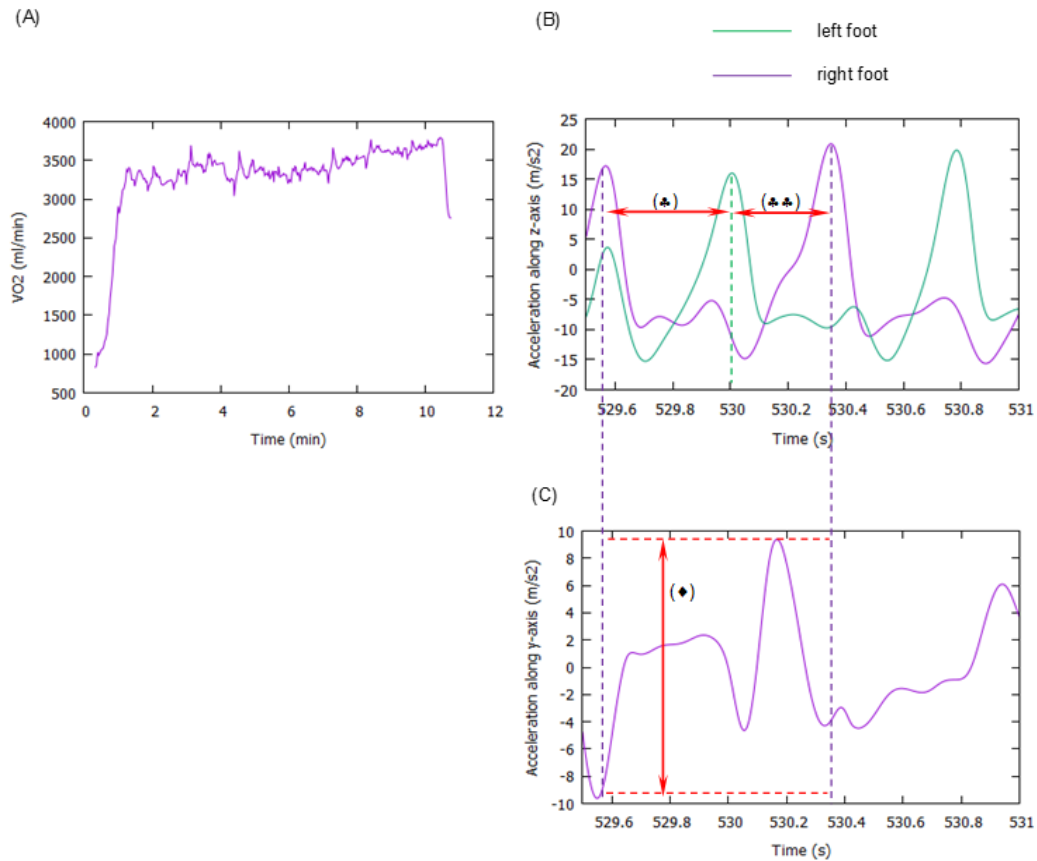


Figure 1. Representative traces of $\dot{V}O_2$ during a running bout after signal filtering (panel A), vertical acceleration signal along z-axis (panel B) and right foot medio-lateral acceleration signal along y-axis (panel C). The right-left step duration is denoted by symbol (*), whereas left-right step duration is denoted by symbol (**). Each full cycle is identified by successive left (or right) peaks. The level of right foot medio-lateral acceleration given by the difference between the maximal value and the minimal acceleration value over the considered full cycle is denoted by symbol (♦).

2.6 Statistical analysis

Data are presented in the text, tables and figures as mean \pm standard deviation (SD). Statistical analyses were performed with Jamovi software (version 1.6). The normality of the data collected for each variable of interest was checked using the Shapiro-Wilk test. In case the data were normal, a paired sample t-test was used to compare each trail condition to its matched treadmill run. If the data were not normal, a Wilcoxon rank test was used. For all statistical analyses, an alpha value of 0.05 was accepted as the level of significance.

3. RESULTS

The running bouts lasted $10:31 \pm 1:18$ min for HT and Sim-HT sessions and $10:51 \pm 1:21$ min for LT and Sim-LT sessions. Therefore, the period of analysis corresponding to 20% to 80% of the total duration had a duration of 6:20 min for HT and Sim-HT and 6:30 min for LT and Sim-LT.

3.1 Oxygen cost of running and RPE

Table 1 and Fig. 2A report the main cardiorespiratory responses. O_2Cr (+10.4% with $p < 0.001$ for LT and +11.4% with $p < 0.001$ for HT) \dot{V}_E (+14.4% with $p = 0.001$ for LT and +28.4% with $p = 0.004$ for HT) and $\dot{V}_E/\dot{V}O_2$ (+8.3% with $p = 0.02$ for LT and +9.2% with $p = 0.03$ for HT) were significantly higher in trail compared to treadmill running. Breathing frequency and $\dot{V}_E/\dot{V}CO_2$ were not significantly different for trail compared to treadmill running (Table 1). HR was significantly greater during HT compared to Sim-HT ($p < 0.001$), but the difference between Sim-LT and LT did not reach the level of significance ($p = 0.08$, Table 1). RPE was not significantly different on trails compared to treadmill running in any condition (Fig. 2B). As expected, perceived technicity was reported to be greater in the field than on treadmill for both conditions (+180.0% with $p < 0.001$ for LT and +264.3% with $p < 0.001$ for HT; Fig. 2C).

Table 1. Cardio-respiratory responses, perceived exertion, step frequency (SF and SFsd) and acceleration (ML and MLsd) for low technicity (LT) and high technicity (HT) trails compared to its matched treadmill runs.

	LT			HT		
	Trail	Treadmill	p-value	Trail	Treadmill	p-value
$O_2 Cr$ (mL/kg/km)	561 ± 31	508 ± 25	< 0.001	587 ± 33	527 ± 28	< 0.001
HR (bpm)	168 ± 15	159 ± 13	0.08	171 ± 13	159 ± 12	< 0.001
\dot{V}_E (L/min)	119 ± 24	104 ± 20	0.001	122 ± 19	95 ± 19	0.004
Breathing Frequency (br/min)	41.3 ± 7.5	40.6 ± 7.7	0.53	44.2 ± 6.8	41.8 ± 7.5	0.16
RER	1.01 ± 0.04	0.95 ± 0.06	0.004	1.02 ± 0.03	0.94 ± 0.05	< 0.001
$\dot{V}_E/\dot{V}O_2$	31.3 ± 4.1	28.9 ± 3.3	0.02	31.9 ± 3.6	29.2 ± 3.1	0.03
$\dot{V}_E/\dot{V}CO_2$	31.0 ± 3.3	30.5 ± 3.0	0.45	31.3 ± 3.6	30.9 ± 2.7	0.69
RPE	11.1 ± 2.1	11.4 ± 1.8	0.68	12.8 ± 0.9	12.4 ± 1.8	0.60
SF (Hz)	2.77 ± 0.15	2.70 ± 0.18	0.89	2.67 ± 0.13	2.80 ± 0.14	0.024
SFsd (Hz)	0.59 ± 0.50	0.19 ± 0.30	0.05	0.47 ± 0.46	0.62 ± 0.54	0.82
ML (m/s^2)	2.40 ± 0.40	1.09 ± 0.25	< 0.001	2.26 ± 0.34	1.06 ± 0.21	< 0.001
MLsd (m/s^2)	2.03 ± 0.41	0.85 ± 0.19	< 0.001	1.88 ± 0.24	0.82 ± 0.17	< 0.001

O_2Cr : oxygen cost of running, HR: Heart Rate, V_E : ventilation, VO_2 : oxygen uptake, VCO_2 : exhaled CO_2 , RER: respiratory exchange ratio, $\dot{V}_E/\dot{V}O_2$: ventilatory equivalent for O_2 ; $\dot{V}_E/\dot{V}CO_2$: ventilatory equivalent for CO_2 , RPE: rating of perceived exertion on a 6-20 Borg scale.

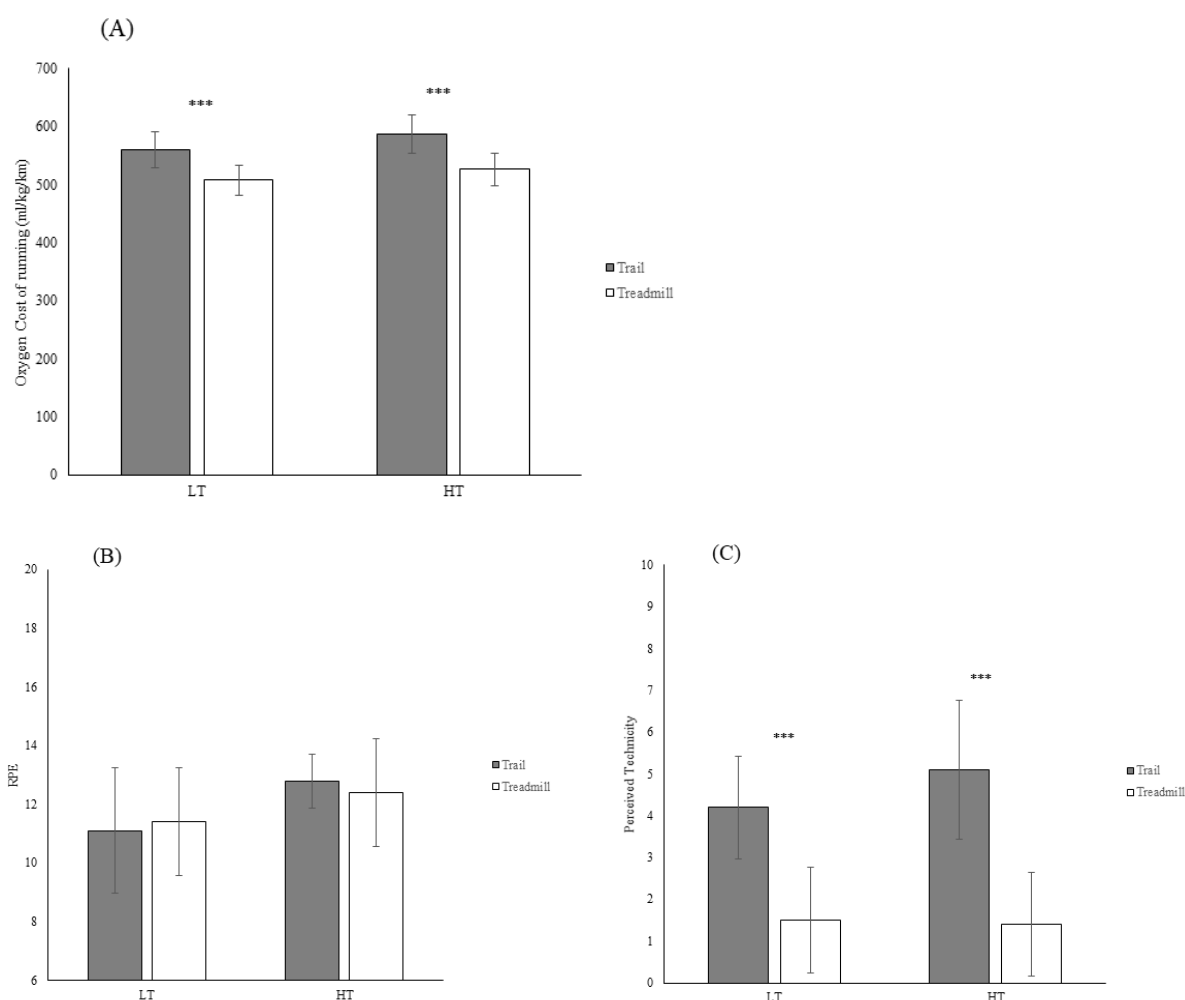


Figure 2. Oxygen cost of running for low technicity (LT) and high technicity (HT) trails compared to its matched treadmill runs (panel A); perceived exertion for low technicity (LT) and high technicity (HT) trails compared to its matched treadmill runs (panel B); perceived technicity for low technicity (LT) and high technicity (HT) trails compared to its matched treadmill runs (panel C). Difference between trail and treadmill, *** $p < 0.001$.

3.2 Running patterns

SF was not different in LT condition when comparing trail vs treadmill running (2.77 ± 0.15 vs 2.70 ± 0.18 Hz, $p = 0.89$, Table 1). However, in HT condition, SF was significantly lower on trail compared to treadmill with a decrease of 4.6%. The variability of step frequency (SFsd) was not significantly different in any condition (Table 1, Fig. 3). The magnitude (ML) and variability (MLsd) of medio-lateral feet acceleration were significantly greater on trail compared to treadmill in both conditions (+117% and +134% for trail compared to treadmill for ML and MLsd, respectively).

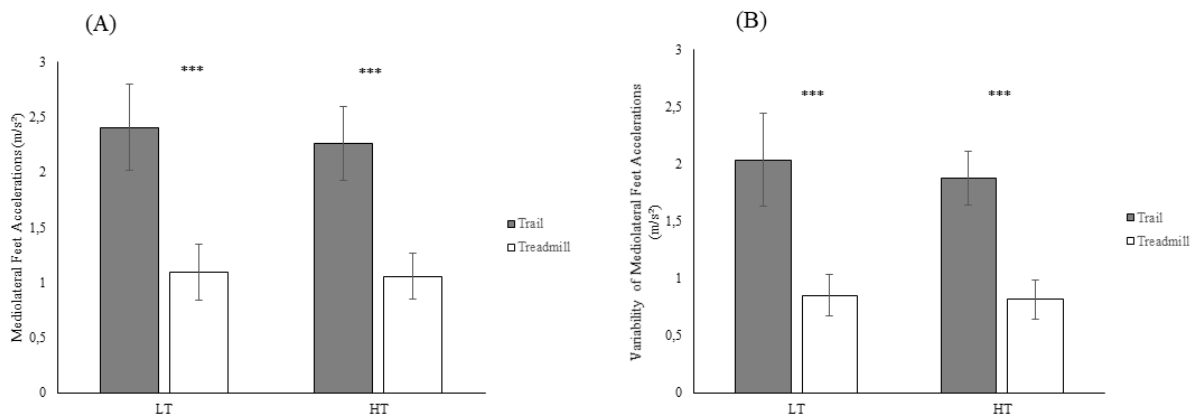


Figure 3. Medio-lateral feet acceleration (panel A) and variability of mediolateral feet acceleration (panel B) for low technicity (LT) and high technicity (HT) trails compared to its matched treadmill runs (difference between trail and treadmill, *** $p < 0.001$).

4. DISCUSSION

The main results of the present study examining the effects of ground technicity during uphill running are that (i) magnitude/variability of feet medio-lateral accelerations as well as (ii) oxygen cost of running, ventilation and heart rate were significantly greater when running on a trail compared to running on a treadmill at a given speed and for a given elevation. However, despite greater cardiorespiratory and biomechanical constraints and enhanced perceived technicity, RPE was not significantly higher when running on the trail.

Physiological parameters and RPE

The present study showed that trail running induces significant physiological alterations as compared to treadmill running. In particular, an 11.4% and 10.4% higher O_2Cr were found in HT and LT conditions, respectively. These changes are higher than those reported by Voloshina and Ferris (2015), who tested subjects on treadmills with and without uneven surface during level running at 2.3 m/s. These authors found a 5% increase in energy demand when running on uneven flat terrain (including stepping areas of different heights, up to 2.5 cm). It is worth mentioning that the average velocity during our tests was slower (1.6 m/s). As discussed below, the overground condition induces specific biomechanical alterations, including lateral deviations of the foot that are thought to participate to the energy expenditure increase. In Voloshina and Ferris' study (2015), it is likely that these lateral deviations were not as large as they could be in the field, due to the specific constraints imposed by the treadmill running conditions which could partly explain why the increase in energy expenditure was smaller in

their study. Moreover, it should be emphasized that our protocol was for uphill running, versus for level running in Voloshina and Ferris' study. As uphill running may induce a greater exertion compared to level running (Vernillo et al., 2017), this could also partly explain the observed discrepancies. Even if not investigated in the present study, it is also probable that uneven overground terrain induces abrupt changes in the vertical position of the center of mass (Ernst et al., 2014), which may contribute to the increase in O_2Cr .

RPE was not different between trail and treadmill running. It has been reported that treadmill running induces greater RPE than during overground level running at a given velocity (Dasilva et al., 2011). In the present study, as O_2Cr was higher on trail, so that one might expect to observe greater RPE on trail too. Moreover, visual solicitation and analysis are required when running on a trail to anticipate and adapt to a constantly changing environment, which may lead to an enhanced attentional cost in the field, and thus to greater RPE. However, we should admit that the affective valence was likely more positive during the overground session than during the treadmill session. Despite RPE was expected to be greater due to a greater O_2Cr , the affective valence of being outdoor may have had a positive effect of the perceived exertion. In other words, RPE might have artificially been enhanced in the laboratory for this reason and other factors such as the absence of landscape, the absence of airflow (i.e. less body cooling), and wearing the mask.

Biomechanical parameters

The present results show that running on trail significantly modifies running patterns as compared to treadmill running. In particular, it is likely that the trajectory should be adjusted with more lateral deviations in order to find the easiest (or safest) path when obstacles are located on trail surface. These lateral deviations are evidenced by the increase in the medio-lateral acceleration variability that stands as an indirect index of the mechanical effort to move the feet along the medio-lateral direction. The increase in O_2Cr (see above) may be due to the change in the muscular activity, as more muscles fibers may be recruited to adjust the trajectory. Additionally, the less stable stance may also require additional motor units recruitment to both stabilize the hip in the mediolateral plane and change the direction of the motion.

It has been previously shown that SF is sensitive to the gradient (Padulo et al., 2012; Giandolini et al., 2016), with SF increasing with the slope. This variable also seems to be affected by the ground technicity as SF was significantly higher on treadmill compared to trail running in HT (4.8% increase), but not in LT, condition. As the velocity on the treadmill was

matched to reproduce the velocity in the field, this also means that step length was likely shortened on treadmill. It is speculated that the runner adjusts to the technicality by increasing the step length to fly over obstacles, even though this induces a higher muscular activity while on the treadmill, the step length is adjusted to optimize muscle activity and cost of running. External perturbations such as uneven terrain continually perturb the running patterns, making each step variable (Seethapathi and Srinivasan, 2019). Surprisingly, the variability of step frequency strongly tended to be different in LT condition (+211% on trail compared to treadmill, $p = 0.05$), but not in HT condition ($p = 0.82$). It was expected that runners would have to constantly adapt spatiotemporal gait parameters to overcome the non-predictability of uneven terrains (Santuz et al., 2018), and that this adaptation would have been more pronounced on the more technical trail. In short, the stride frequency adaptation to technicality is not clear yet, in contrast to running pattern discussed above.

Limitations

Even though comparing ecological trails running against treadmill running provides valuable information to quantify the effect of ground technicality, some limitations should be pointed out. In our study, treadmill was assumed to represent a ‘zero technicality’ condition, as no roughness was present on the treadmill surface, and the subjects were all experienced runners on treadmill. However, treadmill running induces additional artefacts, above discussed, which might affect gait, $\dot{V}O_2$ and RPE. Bassett et al. (1985) reported that HR and $\dot{V}O_2$ measured when running on a horizontal treadmill are higher than those observed during flat overground running at a given velocity (Bassett et al., 1985). This discrepancy, which increases with the velocity, alters the running economy when using a treadmill (Mooses et al., 2015). All these observations highlight the specificities of treadmill running that might have under-estimated the importance of the effect of the terrain condition (vs. treadmill condition) that we have measured on metabolic, biomechanical and perception aspects.

In other words, a comparison with road running would have been preferable even though pacing is more difficult (yet achievable) than on treadmill and environmental conditions (e.g. temperature) would have been much trickier to match with the trail conditions. Indeed, finding outdoor trails that are easily accessible by car or by foot, at a low altitude (lower than 1000 m to avoid potential effects of hypoxia), and that have a regular profile (with no abrupt inclination changes) with homogeneous technicality conditions over a long enough distance (several hundreds of meters) remains a difficult task.

During the field tests, the subjects paced themselves according to the ground technicity, the slope gradient, or other personal factors. It is worth emphasizing that in absence of standardization of the pace for the two trails, direct comparisons between HT and LT condition were difficult. As the velocity affects both the evaluation of RPE and the biomechanical parameters (SF, lateral deviation), it can be inferred that the experimental setting has had an effect on our results and that our findings may not be blindly extended to other running velocities. Moreover, it should be noted that both velocity and grade profiles cannot be reproduced exactly, meter by meter, but only considering each 100 meters segments. Instantaneous running speed was inherently very variable on the trail, and this variability could not be reproduced on the treadmill. This difference in speed profiles, including permanent accelerations and decelerations to adjust to both grade profile and local terrain technicity, could explain a higher oxygen cost on the trail compared to the treadmill.

Finally, accounting for the difference in technicity between the two trails would have been questionable as speed was not clamped. The *a priori* difference in technicity estimated by the investigators was not reported as being significant by the runners. This may also be due to the fact that the running speed was not clamped, giving more ability to the participants to pace and potentially dampen the difference. As a result, the difference is likely too small to make some relevant conclusions.

One purpose of the present manuscript was to quantify the effect of ground technicity on cardiorespiratory, biomechanical and perceptual parameters. Further experiment must extend this first study by replicating these tests on a variety of outdoor trails with *a priori* larger differences in technicity levels and pacing the runners (using for example an electric mountain bike).”

5. CONCLUSION

This paper shows that running on a trail vs. a treadmill significantly affects both O₂Cr and magnitude/variability of feet ML accelerations. Yet, even though lower perceived technicity and O₂Cr were measured on treadmill, RPE was not significantly different as compared to trail running. Ground technicity needs to be further characterized in order to provide objective measurements and to better assess its effects on locomotion from metabolic, biomechanical and perceptive viewpoints. Ground technicity encompasses a variety of features, such as the size and spacing of obstacles, adherence and compactness of the ground, or width

of the trail. Assessing separately the effects of each of these features on the locomotion can be regarded as a stimulating purpose for further studies, in order to get a better understanding of the effects of ground technicity in trail running on cardiorespiratory and biomechanical parameters as it may further emphasize the need to prepare a race by training on a terrain with similar technicity.

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