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Alterations in spontaneous electrical brain activity after an extreme mountain ultramarathon

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ABSTRACT

This study aimed to investigate the impact of an extreme mountain ultramarathon (MUM) on spontaneous electrical brain activity in a group of 16 finishers. By using 4-minute high-density electroencephalographic (EEG) recordings with eyes closed before and after a 330-km race (mean duration: 125 ± 17 h; sleep duration: 7.7 ± 2.9 h), spectral power, source localization and microstate analyses were conducted. After the race, power analyses revealed a centrally localized increase in power in the delta (0.5–3.5 Hz) and theta (4.0–7.5 Hz) frequency bands and a decrease in alpha (8.0–12.0 Hz) power at the parieto-occipital sites. Higher brain activation in the alpha frequency band was observed within the left posterior cingulate cortex, left angular gyrus and visual association areas. Microstate analyses indicated a significant decrease in map C predominance and an increase in the global field power (GFP) for map D at the end of the race. These changes in power patterns and microstate parameters contrast with previously reported findings following short bouts of endurance exercises. We discuss the potential factors that explain lower alpha activity within the parieto-occipital regions and microstate changes after MUMs. In conclusion, high-density EEG resting-state analyses can be recommended to investigate brain adaptations in extreme sporting activities.

1. Introduction

Electroencephalographic (EEG) activity represents the ongoing electrical current generated by discharging neurons and can be captured by electrodes placed on the scalp. Spontaneous EEG activity has been shown to be altered after a bout of several dozen minutes of physical exercise (Kubitz & Pothakos, 1997; Petruzzello & Tate, 1997; Brümmer et al., 2011; Abeln et al., 2015; Gutmann et al., 2015). Exercise studies have reported a global increase in oscillatory activity in all frequency bands—not only alpha waves (Crabbe & Dishman, 2004). Recently, Ciria and collaborators (Ciria et al., 2018, 2019) reported differences in exercise-induced increases between high-to-moderate and light 30-minute aerobic cycling exercises in a wider high-frequency range (8–40 Hz) at parieto-occipital sites. Moreover, the spatiotemporal electrocortical brain dynamics (i.e., time sequences of short-lasting, nonoverlapping patterns of quasi-stable electrical potentials on the scalp) is also modulated after submaximal and time-trial cycling exercises, suggesting specific brain network adaptations (Spring et al., 2017, 2018). However, brain adaptations following prolonged physical activities associated with sleep deprivation have been largely underinvestigated.

Ultratrails running or ultramarathons – defined as any running event over marathon distance conducted in any terrain and surface (Scheer et al., 2020) – represent an exceptional context of investigation to characterize cerebral adaptations to extreme physical load (Millet & Millet, 2012). Ultramarathons have become progressively more popular with an increasing number of practitioners and races offered in the last decade (Scheer, 2019). More athletes are also participating in mountain ultramarathons (MUMs)—which consist of running/walking on mountain trails with positive and negative slopes—where they have to face a number of acute pathophysiological (Knechtle & Nikolaidis, 2018), neuromuscular (Saugy et al., 2013), biomechanical (Vernillo et al., 2014), respiratory (Vernillo et al., 2015), postural (Degache et al., 2014)

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and cardiac (Maufrais et al., 2016) challenges. While psychological, attentional and cognitive failures have been sporadically reported during prolonged endurance races, the neuroelectrical changes in the brain after a MUM have barely been investigated. This study aimed to describe the alterations in spontaneous electrical brain activity in athletes who completed an extreme MUM.

A limited number of studies involving ultraendurance footraces have shown severe dysregulation of emotional states or the quality of sleep (Lahart et al., 2013) but also decreases in cognitive performance (Doppelmayr et al., 2005, 2007; Hurdiel et al., 2015, 2018) as well as dizziness, confusion and visual hallucinations (Glace et al., 2002; Hurdiel et al., 2015). When the duration of the race increases (~300 h), olfactory function—a "surrogate of overall cognitive function" (p. 5)—is negatively affected (Tonacci et al., 2017). Finally, as the footrace becomes incredibly long (i.e., the 4487-km ultramarathon TransEurope Footrace that takes place over 64 consecutive days), a reversible global volume loss of grey matter within specific brain regions that are ordinarily involved in visuospatial and language tasks was reported (Freund et al., 2014). Changes in brain structure and function are not unexpected in these circumstances. When an uninterrupted recurrent task is executed with the overuse of motor and/or cognitive functions for a prolonged period of time, cerebral plasticity spontaneously reorganizes the brain circuitry and adapts to the newly desired behavioural outcome (see Pascual-Leone et al., 2005). Consequently, at a sensory-motor level in particular, after several dozen hours of practice, functional and structural changes within the brain are observed (Kelly & Garavan, 2005; Bezzola et al., 2011). There is little doubt that electrophysiological brain dynamics may change after monotonous physical exercise associated with prolonged sleep deprivation. In a review by Borghini et al. (2014), an increase in theta (4–7 Hz) power was systematically observed for mental workload, fatigue and drowsiness, whereas alpha band (8–12 Hz) modulations depended on the mental state and/or the requirements of the task. In a single-case study, Doppelmayr et al. (2007) evaluated the effect of a 24-h ultramarathon (125 km) on a male athlete. Event-related potentials were assessed using an auditory oddball task one hour before the start and ten times during the race. The results showed an increased latency and decreased amplitude of P300, along with decreased lower alpha power (7–10 Hz) during a quiet period of rest. Another single-case study evaluated EEG changes by comparing three running durations in extreme environments (12, 24 and 56 h) in three different ultramarathons (Doppelmayr et al., 2012). The authors observed a shift in the centre frequency to lower frequencies with increasing running time, which was associated with a reduction in alpha power during the final part of the race (at one electrode over the right parietal region). In these two studies, the authors suggested that participation in an ultramarathon would lead to alterations in attention-related EEG markers at the surface of the scalp.

Although informative, the major limitation of these studies is that isolated electrodes were used to examine electrocortical brain activity, making it impossible to distinguish between source strength or source distribution (see Michel et al., 2009). Applying multichannel EEG (> 64 electrodes) analyses would allow us to differentiate, at the scalp level, the modulations in the activity of the same brain generators (global field power) and changes in the generator distributions (map dissimilarity) and to approximate the intracerebral source localization by computing inverse solutions. Source localization methods can connect surface cortical activity to the Brodmann areas (BAs) or cerebral gyri (Pascual-Marqui, 2002). Thus, it is possible to estimate the locations of the brain-source generators underlying the changes in scalp electrical potentials. A number of studies from Babiloni and coworkers have shown that high-resolution EEG activity recorded during the resting state could detect region-specific changes in spontaneous cortical oscillatory rhythms (mostly in alpha band frequency) in patients with Alzheimer's disease, dementia or mild cognitive impairments (see for example Babiloni et al., 2018). High-density EEG activity recorded at rest is a promising approach to examine the relationships between spontaneous brain states and sport expertise (Babiloni et al., 2010) or acute physical exercise (Schneider et al., 2009; Gutmann et al., 2015; Spring et al., 2017, 2018).

Ongoing broadband EEG activity at rest can show specific and stable (60–150 ms) patterns of scalp potential topographies with archetypal and reproducible temporal properties (e.g. Khanna et al., 2015; Michel & Koenig, 2018). Typically, four topographies/microstates (called maps A, B, C, and D) can be extracted from a multichannel EEG signal that explain approximately 70–80% of the total topographic variance (Brodbeck et al., 2012; Croce et al., 2020; e.g. Koenig et al., 2002; Lehmann et al., 2005; Spring et al., 2017, 2018). Interestingly, map A has been associated with the auditory resting-state network (RSN), map B with the visual RSN, and maps C and D with the salience RSN and the attentional RSN, respectively (Britz et al., 2010). It has also been demonstrated that the topographies that best described the EEG dynamics were spatially highly preserved at different levels of consciousness (i.e. during stages of deep sleep; Brodbeck et al., 2012; Xu et al., 2020). Recently, Spring and collaborators (2017) showed that several temporal parameters of map C were significantly increased after a bout of 30 min of cycling and did not return to baseline during a 60-minute passive recovery period (Spring et al., 2018). Interestingly, the modulation of the mean duration of map C correlated with neuromuscular alterations (Spring et al., 2017). In these two studies, the authors suggested that the postexercise reorganization of the temporal parameters of map C might have reflected the activity of the anterior insula (AI) and the anterior cingulate (ACC) cortices that receive and interpret cardiovascular (i.e., autonomic) and muscle afferences, respectively (AI and ACC are the two neural nodes of the salience RSN; s-RSN; see Menon, 2015). Indeed, during a prolonged physical exercise, body signals from the muscles (via spinothalamocortical pathways) and the cardiac system (via vagal afferents) have their saliency increased within the constant somatosensory and autonomic information flow. Task-related stimuli are detected by the AI which initiates attentional control signals through ACC and dorsolateral prefrontal cortex involved in monitoring, decision-making and cognitive control processing (see Menon & Uddin, 2010). ACC activation has been associated with task difficulty and effort (Paus et al., 1998) and designated as the site for the initiation of behaviors (Craig, 2009). Therefore, the integration of bodily sensations by the ACC in conjunction with motivational and emotional information processed in other regions of the prefrontal cortex (i.e. orbitofrontal cortex) would play a critical role in the regulation of motor control during acute large-muscle physical exercises (Robertson & Marino, 2016). In summary, one of the functions of the salience network, and more particularly via the role of the insula, would be to predict the effects of ongoing/future behaviors on the actual physical/mental resources of the human system (see Gogolla, 2017). The other map of interest in the current study is microstate D. A series of studies attributed map D to a network including the frontoparietal areas sustaining attentional and cognitive control (Britz et al., 2010; Custo et al., 2017; Bréchet et al., 2019). These studies reported an increased duration of map D when resolving mentally arithmetic operations (Bréchet et al., 2019) or serial subtraction (Seitzman et al., 2017) which have been interpreted as the activation of the attentional system, even if conclusive statements about the role of map D should consider the co-modulation of the map C (Seitzman et al., 2017). However, a very recent study reported that the map D duration is increased during episodes of mind-wandering, as compared to verbalization and visualization (Antonova et al., 2022). This conflicting result reveals that further researches are needed to elucidate the functional significance of map D.

In the present study, high-density EEG activity was recorded at rest to investigate electrocortical changes in 16 finishers of one of the most challenging MUMs in the world. In particular, we utilized two surface EEG analyses (in the frequency and spatiotemporal domains) and a complementary source localization analysis. In line with the reported findings from the literature, we would expect—via microstate analyses—specific modulations of the parameters of map C (interoceptive-autonomic processing) and map D (attentional-related marker; see Doppelmayr et al., 2012). In the frequency domain, we hypothesized that there would be a shift towards lower frequencies, which would be characterized by a decrease in alpha waves associated with an increased amplitude at lower frequencies. EEG analyses should reveal changes in brain regions related to the frontoparietal attentional network.

2. Materials and methods

2.1. Participants

Twenty-seven runners were initially enrolled in the study, and sixteen of them (1 female; mean age (yrs): 43 ± 4.9) completed the race (59% of finisher). The recruitment of the participants was made via a letter sent by email by the race organizer informing the runners about the study purposes and the experimental protocol. In addition, the same information was posted on the website of the sporting event. The average finishing time was 125 ± 17 (hours), with approximately 7 h (± 2.9) devoted to sleep (final rank ranged from the 12th to 228th position out of 383 finishers). All participants were experienced in ultramarathoning/trail running, and most of the participants were familiar with the testing procedures, having previously participated in a similar study (Saugy et al., 2013). This study was exploratory, and no control group was employed. The study was approved by the institutional ethics committee of the University of Verona, Italy (Department of Neurological, Neuropsychological, Morphological and Motor Sciences). The experiment was performed in accordance with the ethical standards established in the 1964 Declaration of Helsinki. All participants gave their informed consent prior to their inclusion in the study and were free to stop the experiment at any time without any explanation or any kind of prejudice.

2.2. Procedure

The race supporting this study was the Tor des Géants®. The Tor des Géants® is a 330-km running/walking race with an elevation of approximately 24000 m in Val d'Aoste, Italy. There are 20 passes over 2000 m (maximum and minimum altitudes are 3300 m and 322 m, respectively). The race is divided into seven sections, with six interspersed aid stations where sleeping is allowed. However, each runner can pace himself or herself and is free to rest, knowing that recovery time is not subtracted from the race time. Thus, sleep deprivation and pacing are the overriding parameters determining the final performance.

2.3. EEG recording

Resting EEG activity was recorded for 4 min while the participant was in a sitting position with their eyes closed before the start (PRE) of the race and 45 min after having crossed the finish line (POST) in the same sound- and lighted-attenuated room (Courmayeur, Italy; altitude: 1224 m). Close to the finishing area, an experimenter was waiting to pick up the runner and to guide her/him to the experimental room (10 min' walk) for completing the tests. The runner was allowed to talk few minutes with friends and family members, to drink and wear dry and warm clothes if necessary. They were not allowed to have a nap. This took around 45 min, a time interval the team of experimenters decided to apply not to thwart the runner. Importantly, this duration corresponds to the time window for full cardiac recovery. Indeed, it has been shown on this mountain ultramarathon, that resting heart rate was similar between pre- (55 ± 8 bpm) and post-race measurement (59 ± 8 bpm), particularly since the recording was performed later (45 min) than in Maufrais and collaborators (2016); i.e. (37 ± 17 min). This pattern of HR adaptation was observed only during this type of mountain ultramarathon event and not during shorter ultra-endurance events (e.g. marathon, ironman triathlon). Therefore, we are confident that 45 min was enough for the HR values to return to baseline, which make the cardio-respiratory states for EEG recordings comparable before and after the race. During the recordings, the experimenter checked the position and movements of the head. When signs of falling asleep were observed, the experimenters lightly touched the shoulder of the participant to help her or him stay awake. A 64-channel Biosemi ActiveTwo amplifier system (Biosemi, Amsterdam, Netherlands), referenced to the CMS-DRL ground that functions as a feedback loop driving the average potential across the montage as close as possible to amplifier zero, was used for data acquisition. An EEG cap (Electrocap International, Inc., USA) built of 64 Ag-AgCl electrodes was mounted and adapted to the individual's head size according to the 10–20 System. Electrodes were filled with an electrogel for optimal signal transduction, and the impedance was kept below 5 kΩ.

One might wonder if the altitude of PRE and POST sessions (1224 m) can influence the spontaneous EEG activity, due to the fact that the brain is sensitive to the cerebral oxygen delivery. The literature reports electrocortical adaptations in simulated or real altitude conditions. Acute exposure to hypoxia (< 1-hour) reveals a slowing in EEG signal (higher theta power for example) and inconsistent modulations within the alpha bands (Kraaier et al., 1988; Ozaki et al., 1995; Papadelis et al., 2007). For longer exposure durations, two studies reported different patterns of power changes with the increasing acclimatization time (Zhao et al., 2016). However, such significant oscillatory modulations at rest have been observed at very high altitude only (>6000 m) but not at 5000 m (Papadelis et al., 2007) and some authors reported that the saturation of oxygen should be lower that 75% (altitude >5000 m) to observe strong impairments at the neuronal activity level (see Goodall et al., 2014). By consequence, we assume that the EEG recordings in the current study were not altered. At the altitude of 1224 m, the bioelectrical adjustments at the brain level should be negligible.

2.4. EEG analyses

2.4.1. Power spectral density analyses

The surface EEG data were analyzed with BrainVision Analyzer software (Brain Products, München, Germany). Raw EEG data were first down-sampled from 2048 to 1024 Hz to reduce the computational load. Secondly, we interpolated visually-identified bad electrodes and high- and low-pass filters were applied with a frequency range from 0.5 to 49 Hz (time constant 0.3183 s; 24 dB/octave). The first and last 30 s were discarded to remove the entering and exit effects into the resting task respectively, and the remaining 180 s signal was then segmented into 3-s sections with an overlap of 10%. The semiautomatic artifact rejection was set to a gradient < 50 μV (ICA application in Analyzer 2, Brain Products, München, Germany) to identify and delete eye-blinks as well as muscular artifacts. For the statistical analyses, three regions of interest were selected (ROI1: frontal AF3, AFz, AF4; ROI2: central C1, Cz, C2; ROI3: parieto-occipital PO3, POz, PO4) in the delta (0.5–3.5 Hz), theta (4–7.5 Hz) and alpha (8–12 Hz) frequency bands. Due to the absence of normality by the inter-participant and inter-electrode variations in absolute spectral power values, the original power spectral density data were log transformed for normalization.

2.4.2. Source electrical estimations

A standardized low-resolution electromagnetic tomography method (sLORETA; University Hospital of Psychiatry, Zurich, Switzerland; http://www.uzh.ch/keyinst/loreta.htm) was applied to determine the neural generators responsible for the power differences observed between the PRE and POST conditions. sLORETA is a linear inverse imaging method that is obtained by standardizing a minimal norm inverse solution by source variance and measurement noise (see Pascual-Marqui, 2002). It is based on a probabilistic Montreal Neurological Institute (MNI) brain volume, which was scanned at a 5 mm resolution, providing 6239 voxels. Coordinates given within this study will refer to the MNI 152 template and allow for the possible identification of generator activation linked to the Brodmann areas (BAs) and brain structures. After down-sampling the filtered data to 256 Hz and applying the average reference, the 180-s signal was segmented in a minimum of 30 epochs (4 s duration each) of artifact-free EEG. An average was applied to calculate cross-spectra in sLORETA for the delta (0.5–3.5 Hz), theta (4–7.5 Hz), alpha (8–12 Hz) bands for each participant, using the sLORETA transformation matrix. Cross-spectra of each participant and for each frequency band were then transformed to sLORETA files. This resulted in the corresponding 3D cortical distribution of the electrical neuronal generators for each participant.

2.4.3. *Microstate analyses*

Microstate analyses were performed with the Cartool software developed by Denis Brunet (Brunet et al., 2011). The two initial datasets (PRE and POST conditions) were preprocessed separately. The raw EEG signal was bandpass filtered between 1 and 40 Hz and visually inspected. Periods of muscular artifacts were manually excluded, and infomax-based independent component analysis (ICA) was applied to remove eye-blinks and cardiac artifacts based on the topography, the waveform, and the time course of the ICA component (Jung et al., 2000). The signal was down-sampled to 128 Hz, and bad electrodes were interpolated using a 3-D spherical spline and recomputed to the common average reference. The global field power (GFP) used in the microstate analysis reflects the strength of the scalp potential field and corresponds to the standard deviation of all electrodes at a given time point. Because the local maxima of the GFP represent an optimal signal-to-noise ratio (Pascual-Marqui et al., 1995), the EEG signal was marked at the corresponding time frame of the GFP peaks. Then, only the time points of GFP peaks were submitted to k-means clustering analysis (Pascual-Marqui et al., 1995; Murray et al., 2008) to identify the most representative classes of stable topographies. Note that the GFP peaks that were visually identifiable within periods of residual artifacts were manually excluded. The two preprocessed EEG datasets (PRE and POST conditions) of each individual were then concatenated into one file and submitted to k-means clustering to identify the spatial topographies that maximally explained the variance of the map topographies (for technical issues, see Michel et al., 2009). In the second step, the best representative microstates of each participant were used to generate a grand clustering to obtain the optimal number of clusters at the group level (i.e., the 4 conventional map topographies). These four maps were then used as templates. The spatial correlation was computed between the map topographies within the initial preprocessed EEG dataset of each participant in the two conditions (PRE and POST) and the 4 representative map templates identified by the grand clustering. Each topography was labeled as the microstate class that was most closely correlated (Brunet et al., 2011). Temporal smoothing parameters (window (half) size) = 3; strength (Besag(10)) were fixed to avoid excessive artificial interruptions in segments because of a low GFP. This fitting process generates the temporal microstate parameters for the four classes, such as the global explained variance (GEV, the sum of the explained variances of each microstate weighted by the global field power), the mean duration (average time in milliseconds covered by a given microstate), the time coverage (percentage of the time covered by a given microstate), and the frequency of occurrence (mean number of the occurrence of a distinct microstate within 1 s). Mean GFP and the GFP peak (the strength of the electric dipoles at the origin of a given microstate) were also computed.

2.5. *Statistical analyses*

For the power and microstate analyses, statistical tests were performed with Statistica version 13.3 (TIBCO Software Inc. (2017), Palo Alto CA, USA, http://statistica.io). The normality of the distributions was controlled using a Kolmogorov-Smirnov test ($p < 0.05$). To examine exercise-induced changes in surface-EEG activity, a two-way repeated-measure ANOVA, ROI (ROI1, ROI2, ROI3) x TIME (PRE vs. POST), was computed for each band of frequency. Concerning the microstate parameters, two-way ANOVA of 2 (TIME) x 4(MAP) were computed. Bonferroni post-hoc tests were used when necessary. The significance threshold was fixed at $p < 0.05$. Effect sizes were computed using partial eta-squared (η_p^2). At the source estimation level, paired samples t-tests were computed at each voxel. Statistical significance was assessed using a nonparametric randomization test (5′000 permutations). To correct for multiple comparisons, a nonparametric single-threshold test was used to define a critical threshold ($t_{critical}$). Voxels with values exceeding this threshold were considered as significantly different. These voxel-to-voxel values are displayed as statistical parametric maps. All the significance thresholds were fixed at $p = 0.05$.

3. Results

3.1. *Power spectral density*

In the delta band, ANOVA showed a significant main effect of ROI, (F(2,30)= 62.75; $p < 0.0001$; $\eta_p^2 = 0.80$), a significant main effect of TIME (F(1,15)= 12.45; $p = 0.003$; $\eta_p^2 = 0.45$) and a significant interaction between ROI and TIME (F(2,30)= 5.13; $p = 0.012$; $\eta_p^2 = 0.25$). In the theta band, the statistical analysis indicated significant main effects of ROI (F(2,30)= 6.84; $p = 0.003$; $\eta_p^2 = 0.31$) and TIME (F(1,15)= 9.72; $p = 0.007$; $\eta_p^2 = 0.39$), as well as a significant interaction between ROI and TIME (F(2,30)= 7.13; $p = 0.0029$; $\eta_p^2 = 0.32$). In the delta and theta bands, the post-hoc tests indicated a more important power increase for the central ROI2 in the POST condition (Fig. 1A-B). In the alpha band, ANOVA showed a significant main effect of ROI (F(2,30)= 87.31; $p < 0.0001$; $\eta_p^2 = 0.85$) and a significant main effect of TIME (F(1,15)= 11.94; $p = 0.003$; $\eta_p^2 = 0.44$). The interaction between ROI and TIME (F(2,30)= 23.69; $p < 0.0001$; $\eta_p^2 = 0.69$) revealed that the power decrease was significantly more important in the POST condition for the parieto-occipital ROI3 (Fig. 1 C).

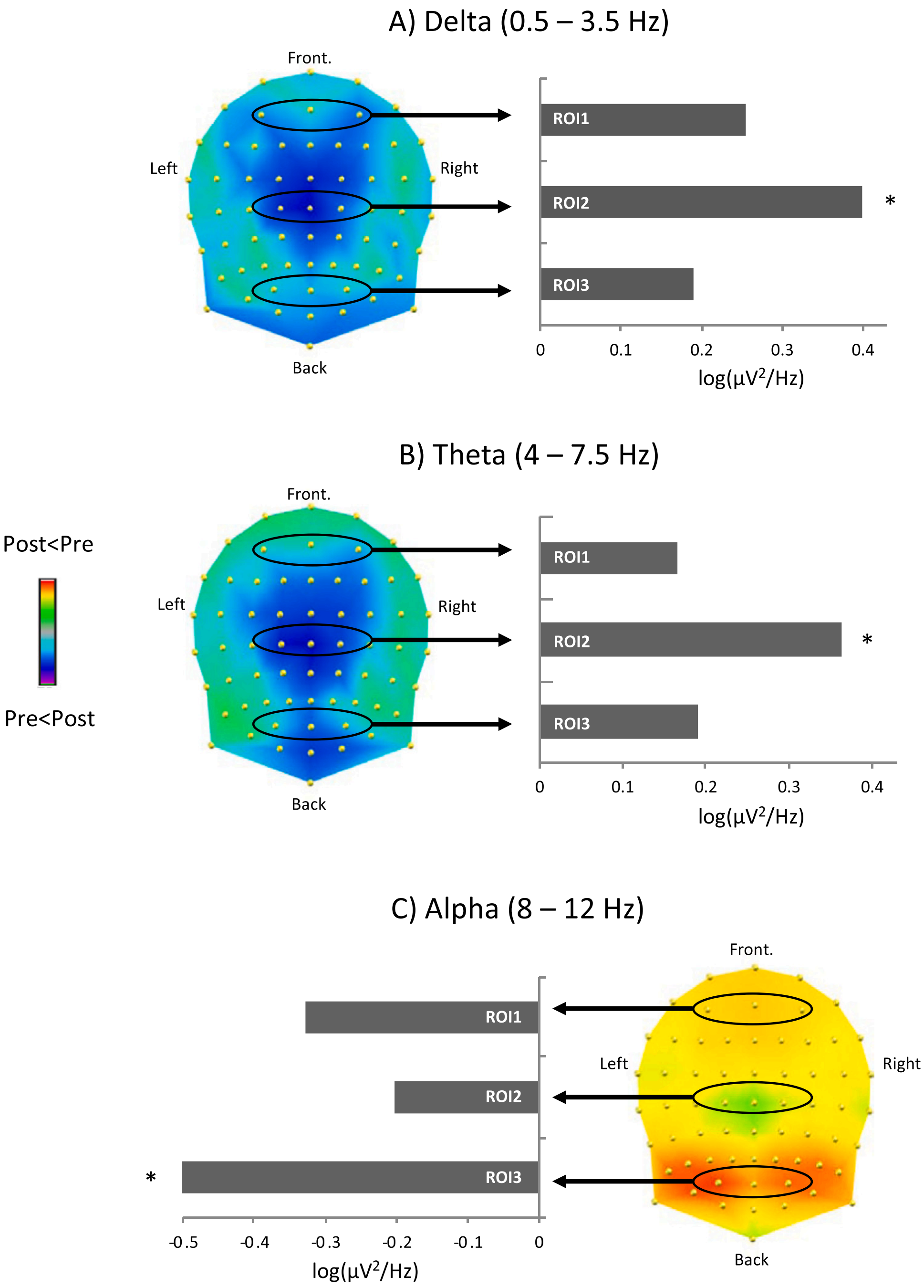
3.2. *Source localization estimations*

Comparison of source estimation data recorded before (PRE) and after exercise (POST) showed, in alpha frequency band (8–12 Hz), a significant increase of activation ($t_{critical}$ for $p < 0.05 = 1.112$) in the left posterior cingulate cortex (BAs 30 and 31), the left angular gyrus (BA 39) and within the occipital lobe (BAs 18 and 19) (see Table 1 and Fig. 2). The highest significance was found at the MNI coordinates x, y, $z = -35, -75, 25$ (BA 19 in left temporal lobe). The cluster size of the five largest clusters (BAs 18, 19, 30, 31, and 39) that showed a supra-threshold t-value was 17.9 cm^3. No further significant changes were observed for the delta and theta frequencies.

3.3. *Microstate analysis*

The four microstates obtained in the analysis explained more than 80% of the global variance and were labeled as classes A, B, C and D in accordance with the literature (Brodbeck et al., 2012; Croce et al., 2020; e.g. Koenig et al., 2002; Lehmann et al., 2005; Spring et al., 2017, 2018). ANOVA showed a main effect of TIME for the mean duration (F(1,15)= 12.16; $p = 0.0033$; $\eta_p^2 = 0.44$) and the frequency of occurrence (F(1,15)= 5.56; $p = 0.031$; $\eta_p^2 = 0.27$). A main effect of MAP was obtained for each parameter (GEV, F(3,45)= 38.69; $p < 0.0001$; $\eta_p^2 = 0.72$; peak GFP, F(3,45)= 11.32; $p < 0.0001$; $\eta_p^2 = 0.43$; mean GFP, F(3,45)= 16.68; $p < 0.0001$; $\eta_p^2 = 0.52$; mean duration, F(3,45)= 39.28; $p < 0.0001$; $\eta_p^2 = 0.72$; time coverage, F(3,45)= 44.53; $p < 0.0001$; $\eta_p^2 = 0.74$; and frequency of occurrence, F(3,45)= 29.19; $p < 0.0001$; $\eta_p^2 = 0.66$). For all parameters, the main effect of MAP indicated that the values were significantly increased for map C compared to the three other maps.

Significant TIME x MAP interactions were obtained for all of the variables (GEV: F(3,45)= 7.06; $p = 0.0005$; $\eta_p^2 = 0.32$, peak GFP: F



A) Delta (0.5 – 3.5 Hz)

B) Theta (4 – 7.5 Hz)

C) Alpha (8 – 12 Hz)

Fig. 1. A) Topographic map (left) of EEG power ($\log(\mu V^2/Hz)$) and bar graphs (right) in delta band (0.5–3.5 Hz) of the difference between PRE and POST conditions. The bar graphs (right) represent mean value of the difference according to the three ROIs (frontal ROI1, central ROI2 and parieto-occipital ROI3). Positive data indicate power value in POST greater than power value in PRE. B) Topography map and bar graphs of EEG power difference ($\log(\mu V^2/Hz)$) in theta band (4.0–7.5 Hz). C) Topography map and bar graphs of EEG power difference ($\log(\mu V^2/Hz)$) in alpha band (8.0–12.0 Hz). Red color indicates decreased power in the POST condition and blue color increased power. * illustrates the origin of the ROI x TIME interaction in each frequency band ($p < 0.05$).

(3,45)= 3.19; $p = 0.032$; $\eta_p^2 = 0.17$, mean GFP: F(3,45)= 9.50; $p < 0.0001$; $\eta_p^2 = 0.38$, mean duration: F(3,45)= 6.11; $p = 0.001$; $\eta_p^2 = 0.28$, and time coverage: F(3,45)= 4.47; $p = 0.007$; $\eta_p^2 = 0.22$) except for the frequency of occurrence (F(3,45)= 0.92; $p = 0.43$). Post hoc comparisons revealed a significant decrease from the PRE to POST sessions for map C concerning GEV ($p = 0.0017$), mean duration ($p < 0.0001$) and time coverage ($p = 0.045$). A significant increase between the PRE and POST sessions was observed for map D concerning peak GFP ($p < 0.0001$) and mean GFP ($p = 0.0006$). The results for the mean duration, the time coverage and GFP max are illustrated in Fig. 3.

4. Discussion

To our knowledge, the present study is the first to investigate the effect of a MUM on spontaneous brain activity in a group of runners by applying complementary EEG analyses: 1) a surface power analysis based on three regions of interest; 2) a source localization method for identifying source generators; and 3) a microstate analysis. The main findings regarding the scalp oscillatory activity were increased delta and theta powers over the central region, and decreased alpha power over the parieto-occipital region after the race. Since a reduction in alpha rhythm amplitudes is considered as a functional correlate of cortical activation (see Klimesch et al., 2007), the results obtained at the scalp level are fitting with those found at the source level. The only significant result from the source estimation analyses was observed in the alpha frequency band and revealed an increased activation within the left posterior cingulate cortex (left PCC), the left angular gyrus (left AG) and the associated visual regions. Finally, microstate analyses showed significant decreases in the mean duration, time coverage and global explained variance in map C and a significant increase in the global field

Table 1
Brodmann's areas that showed a significant decreased ($p < 0.05$)[1] in alpha activity (8–12 Hz) PRE versus POST sessions with sLORETA.

Brodmann's Area	No. Voxels ($p < 0.05$)[2]	cm^3
19	51	6.38
39	50	6.25
18	21	2.63
31	11	1.38
30	10	1.25
17	4	0.5
22	4	0.5
37	3	0.38
7	1	0.13
23	1	0.13

[1] Significance was defined as a *t*-value exceeding the threshold of $p < 0.05$ ($t_{critical} = 1.112$)

[2] sLORETA voxel size is 5 x 5 x 5 mm

power (GFP; strength of the electric field) for map D.

The increased power in the theta and delta bands was similar to the typical spectral modulations observed at sleep onset or non-REM stages for delta activity (Merica & Fortune, 2004) or in fatigued participants during a simulated driving task (Craig et al., 2012) for the theta frequency bands. However, the prominent decrease in alpha power (lower alpha amplitude) in the parieto-occipital regions observed in our results differed from studies on fatigue symptoms (Craig et al., 2012) and on the posttest effect following single bouts of endurance physical exercise (Ciria et al., 2019; Crabbe & Dishman, 2004). In the former, EEG recordings revealed increased amplitudes in the theta and alpha frequency bands but not in the delta band in participants with strong symptoms of fatigue (i.e., tiredness, fatigue-related facial behaviours, and difficulty concentrating) but without physical fatigue or sleep disorders. In the latter, the reviewed studies in Crabbe and Dishman (2004) have reported either an increase in alpha amplitude (when expressed as absolute values) or an absence of changes when oscillatory changes in alpha bands were assessed relative to activity in other frequency bands. In addition, this review also reported that the changes are not restricted to alpha frequency bands or to specific brain regions (see also Spring et al., 2017). Of note, all the studies included examined electrocortical brain changes for exercises lasting from 2 to 60 min. More recently, Ciria et al. (2019) showed an increase in power over a wider range of frequencies (8–40 Hz) at parieto-occipital locations following a 20-minute vigorous cycling exercise compared to a light cycling exercise. Our results are, however, in line with the global increase in power at lower frequencies (1–5 Hz) obtained in the study of Ciria and collaborators.

The physiological and psychological mechanisms that contribute to resting EEG changes after acute exercise are complex and difficult to disentangle. However, some explanations like the role of the catecholaminergic arousal system on the electrocortical modulations have been raised. The release of noradrenaline, dopamine and serotonin during acute physical exercise would promote the activation of the thalamocortical feedback loops that regulate rhythmicity at the cortical and subcortical levels which alter mental states and the feeling of fatigue (see Dietrich & Audiffren, 2011 for a review). For example, it was reported that exercise-related changes in noradrenergic activity is closely associated with modulations of power spectrum in alpha and beta frequency bands (Nieuwenhuis et al., 2005) and that, after a resistance exercise, plasma norepinephrine level is correlated with low alpha and low beta activity (Stock et al., 1996). Moreover, the serotoninergic system projecting widely its neural connections throughout the brain would be involved in cortical deactivation (Dietrich & Audiffren, 2011). Finally, the rise of body temperature – a correlate of increased metabolism during exercise – is related to the ratio of alpha activity to beta activity in the frontal regions (Nielsen et al., 2001). Complementary to the neurotransmitter hypothesis as an explanation of the effect of exercise on brain activity, it is worth mentioning the concept of exercise-induced transient hypofrontality (Dietrich, 2006). This neurocognitive concept supports the idea of a reallocation of the brain's resources to sustain the neural activation of motor, sensory and autonomic systems with a concomitant deactivation of the neural structures that are not crucial during an acute physical exercise (mainly the frontal regions that are occupy by cognitive functions). A bulk of researches have pointed out increased alpha activity (which correspond to cerebral deactivation) in the frontal regions after exercising (Petruzzello & Landers, 1994; Kubitz & Pothakos, 1997). Even if we did not find an increased activity in the alpha band over the frontal regions, the major mechanism to keep in mind with this concept is the reallocation of the cerebral resources to optimize the motor and mental processes all along the MUM. It is doubtless a key mechanism of the athlete's brain to dynamically regulate emotional, cognitive, motor, but also metabolic systems along a prolonged endurance exercise. However, it is difficult to assert that the effect of brain's resources reallocation on the EEG signal is still visible after crossing the finish line. At a more psychological level, a clear relationship between mood dimensions and EEG activity have been observed (Schneider et al., 2009). These authors showed that resting alpha activity relates to changes in perceived physical state while changes in higher frequency bands are associated to perceived

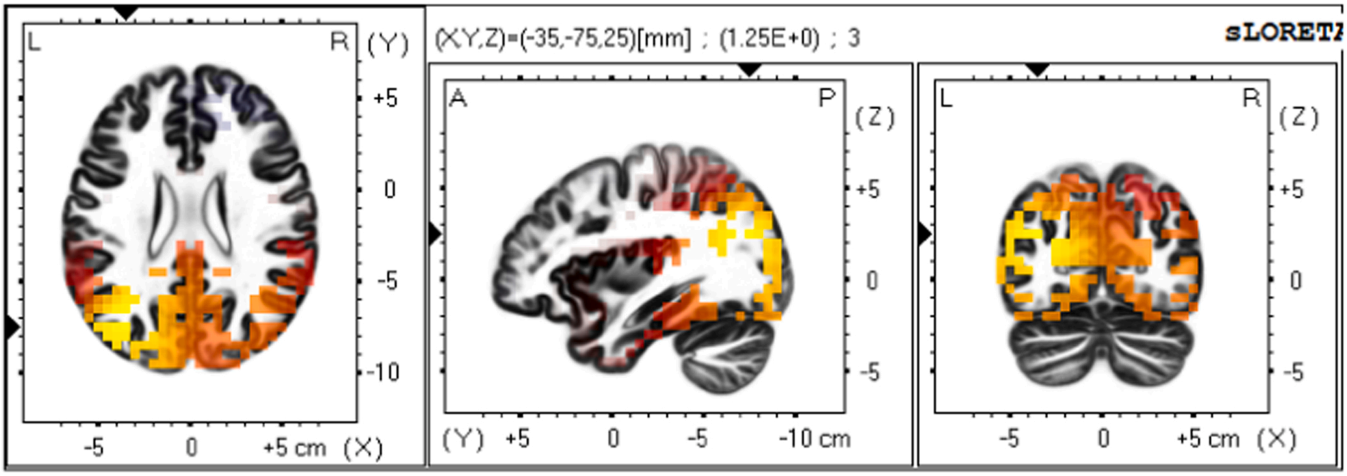


Fig. 2. Statistical parametric maps of sLORETA differences comparing PRE versus POST sessions in alpha (8–12 Hz) activity centred at the highest significant voxel ($x, y, z = -35, -75, 25$; BA 19 in left temporal lobe). Maps are based on voxel-by-voxel *t*-value of differences. Left to right: slices in axial (top, nose up), sagittal (left) and coronal (back) views. A = anterior; P = posterior; L = left; R = right. Yellow and red colours indicate an increased activation in the POST session, which was found significant in BAs 18, 19, 30 and 31.

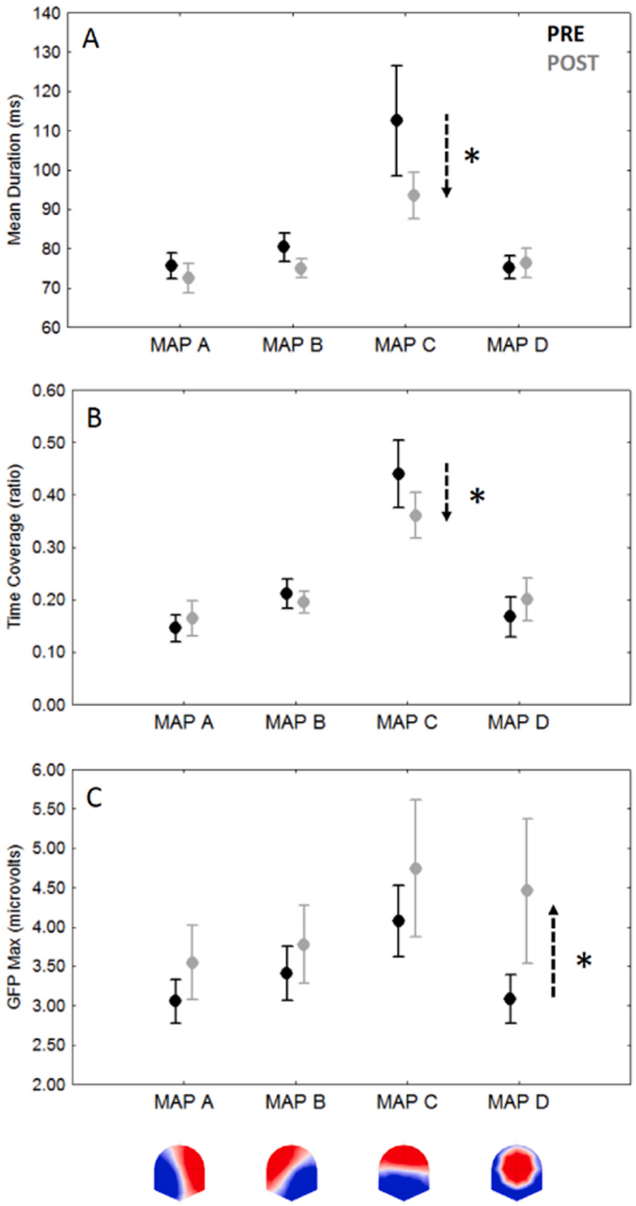


Fig. 3. Microstates parameters of maps A, B, C and D recorded before (PRE; black filled circle) and after (POST; grey filled circle) the race. The mean duration (A) and the time coverage (B) of microstate C significantly decrease at POST. The mean GFP (C) of the microstate D significantly increase at POST. Error bars indicate the standard deviation. * indicates significant difference at $p < 0.05$.

motivation state and psychological strain whatever the intensity of exercise.

In ultralong duration exercise, when sleep deprivation has to be considered, the EEG literature is essentially nonexistent. A single-case study revealed a shift in the centre of gravity of the alpha frequency to lower frequencies as a function of time (comparisons between 12-, 24-, 56-h ultramarathons) but not a systematic decrease in the alpha amplitude (Doppelmayr et al., 2012). Notably, Gutmann and collaborators (2015) found a shift of the alpha peak in the other direction (i.e., to higher frequencies) immediately after completing a short-lasting exhaustive physical exercise. Our results established that running for more than 100 h significantly reduced alpha power, which lessens Doppelmayr's conclusion that the alpha amplitude would be relatively insensitive to exhaustion due to exercise duration. In summary, our results and previous results have indicated that the impact of ultraendurance races on brain rhythms contrasts with changes in brain oscillatory activity induced by short endurance exercises. It is worth noting that the exercises intensity of the support MUM of this research was estimated in previous studies of our group and corresponds on average to 40–50% of VO_{2peak} (Maufrais et al., 2016) and to 50–67% VO_{2peak} when we consider only the uphill sections (Savoldelli et al., 2017). This shows that such ultra-distance events rely exclusively on aerobic energy pathway. Of primary importance is also the biphasic responses observed only on these types of MUM and not on shorter endurance events. Many physiological responses are largely different between the first and the second half of the race since there is a large (~30%) decrease in velocity (Saugy et al., 2013; Maufrais et al., 2016). A similar decrease in intensity was also shown by the changes in vertical speed (m/h) measured only during the uphill portion of the mountain passes throughout the race (Jeker et al., 2020). This biphasic response was observed in cardiac biomarkers (Le Goff et al., 2022), cardiac fatigue (Maufrais et al., 2016) or alterations in postural control (Degache et al., 2019) and is a consequence of several mechanisms including the large decrease in exercise intensity mainly due to sleep deprivation and the large increase in extracellular water. One cannot rule out that the increase in hydric - more specifically extracellular water at distal levels as calves (Vitiello et al., 2015) or brain inter-cellular water content (Zanchi et al., 2017) that are specific of such extreme MUM are also impacting the electrical brain activity investigated in the present study.

In ultramarathons, sleep deprivation likely has a strong effect on functional brain reorganization. Indeed, the specific EEG patterns observed here (i.e., increased delta and theta power and decreased alpha power in the parieto-occipital regions) resembles the findings of del Percio and collaborators (2019) and strongly suggests a high motivation for sleeping. It has been well documented that at the onset of drowsiness, alpha rhythms attenuate or diminish for a few seconds and reappear again for a few minutes until the trains of alpha waves completely disappear at the onset of sleep, along with a gradual increase in theta power (Smith et al., 2002; Strijkstra et al., 2003). The local power modulation shown in our results with a massive mediocentral increase in the delta and theta amplitudes partly mimics the EEG patterns observed with sleep phenomena, although from sleep onset, low-frequency activity is expected to be more prominent at the anterior sites of the scalp (Marzano et al., 2013). Thus, we assume that the participants were in an intermediate state of consciousness between waking and sleeping, which is often associated with hypnagogic imagery (McKellar & Simpson, 1954). This modified brain state could be fertile ground for visual hallucinations that are reported in 25–30% of athletes during ultratrails running (Dahl, 2015; Hurdiel et al., 2015; Mojica, 2003). This assumption is further supported by our results from the source localization analysis. Indeed, after the race, our results displayed increased activation within the visual association cortices (BAs 18 and 19). In a recent meta-analysis of the neural mechanisms of hallucinations, Zmigrod et al (2016) observed hyperactivation of the extrastriate visual areas, dorsal cuneus and precuneus while individuals were experiencing visual hallucinations. In addition, sleep deprivation-induced hallucinations result in increased excitability of the extrastriate visual areas (Sireteanu et al., 2008).

Moreover, hyperactivation of visual areas, which is expressed as decreased alpha band power at rest with eyes closed, has also been reported after a mental fatigue-inducing task (Ishii et al., 2013). Overactivation of the visual regions has been interpreted by Ischii and colleagues as a compensatory mechanism to maintain the efficacy of the information processing required to perform the task despite the growing fatigue induced by a prolonged/heavy workload. Because they also observed that the reduction in alpha power was negatively correlated with an index of sympathetic nerve activity (low-frequency to high-frequency power ratio (LF/HF)), these authors proposed that decreased alpha band power was a marker of mental fatigue. Interestingly, alpha activity reductions induced by sleep deprivation were much less prominent if a single dose of a vigilance-enhancing drug was administered (Del Percio et al., 2019). This result is in line with Barry et al (2007) who stated that changes in alpha amplitude in the eyes-closed resting condition indicate modulation of arousal/vigilance. Finally, it is worth noting a link between alpha activity in the occipital regions and caffeine intake (Barry et al., 2011). Hence, it is likely that soon after finishing the MUM, runners would still present raised sympathetic tone and elevated levels of psychostimulant-like neurochemicals that could participate in the lowering of alpha activity. However, it is challenging to assert whether posttest overactivation within the occipital regions is a reflection of compensation for impaired processing efficacy, an increase in vigilance due to circulating catecholamines and other psychostimulants, a brain state inducing visual hallucinations or a combination of all of them.

Our results also revealed increased activation within the left AG and the left PCC. The AG—one of the key connector hubs linking the different subsystems and integrating information between different modalities—is engaged in "*the manipulation of conceptual knowledge and mental representations when the mind wanders during rest*" (Seghier, 2013 p. 49), and is also engaged in a wide range of tasks involving spatial cognition (such as the ability to discriminate left and right in reading processing). As an integral part of the default mode network (DMN) (see for example Buckner et al., 2008), the dorsal PCC has been determined to play a significant role in maintaining a broad attentional focus during periods of rest (Leech et al., 2012). The increased activation of the dorsal PCC after the race might indicate changes in a subregion of the DMN, which could reflect an altered functioning of the attentional mechanisms and/or arousal in line with Doppelmayr's conclusions (2007, 2012) and our hypotheses. This is supported by the microstate analysis that showed an increase in the GFP parameters for map D, a topography that has been negatively correlated with the blood oxygen level-dependent (BOLD) functional magnetic resonance imaging signal within the frontoparietal attentional network (Britz et al., 2010). Interestingly, a very recent study reported that map D duration is increased during episodes of mind-wandering, as compared to verbalization and visualization (Antonova et al., 2022). This variation in the signal arising from that network can be interpreted as an altered capacity in mobilizing attentional resources after the MUM even if a direct link between the attentional system and microstate D remains to be confirmed (Seitzman et al., 2017).

In line with our expectations, the microstate analyses revealed postrace alterations in the temporal parameters associated with map C. While Spring and collaborators (2017, 2018) reported significant increases in the mean duration, time coverage and global explained variance after less than one hour of physical exercise, the current results revealed opposite findings (i.e., significant decreases in the mean duration and time coverage for map C). Based on the studies of Britz and collaborators (2010) and Custo and collaborators (2017) that have shown a link between map C and brain regions constituting the s-RSN (anterior cingulate and insular cortices), Spring and collaborators proposed that postexercise microstate C modulations may rely on the functional connections between the s-RSN, the autonomic cardiovascular system and multiple sources of afferent signaling pathways or peripheral cues. The s-RSN is a connected, large-scale network anchored in the AI and dorsal part of the anterior cingulate cortex (dACC) (Menon & Uddin, 2010; Menon, 2015), in which the AI plays a central role in the processing of muscular and cardiac inputs but also of endogenous markers of peripheral inflammation, such as cytokines (see Dantzer et al., 2014 for a review about the neuroimmune basis of fatigue). Interestingly, another neuroinflammatory marker induced by physical exercise (interleukin-6; IL-6) has been proposed to be a key messenger signaling the sensation of fatigue to the brain (Vargas & Marino, 2014). A more recent study from the same research group has pointed out a link between IL-6 and the electrocortical activity changes (Vargas & Marino, 2018). A comprehensive review by Gogolla (2017) supported the central role of the insula in the monitoring of the environment, feelings/emotions and perception of bodily states. Complementary to this point, the transit of peripheral information to the motor cortex via the insula has been related to increased communication between these regions after fatiguing cycling exercise (Hilty et al., 2011).

Globally, one may speculate that following a prolonged endurance race associated with sleep deprivation, the s-RSN would become less prominent within electrocortical brain dynamics. We could presume that in ordinary conditions of time-limited exercise—even at high intensity (see Spring et al., 2017, 2018)—this network may contribute to behavioural adaptations (e.g., by reducing the central motor drive to avoid any threats to the body) based on exercise-induced interoceptive-autonomic feedback. This adaptive brain mechanism could be reflected by an increase in the stability and dominance of map C. In contrast, despite muscular metabolic accumulation, inflammatory messages, cognitive/perceptual impairments and small bodily injuries, the CNS may become progressively less sensitive to these negative feedback loops to make the physical effort more tolerable. At the brain level and in the hours following the race, such a functional response could be detectable by a decreased predominance of map C within the electrocortical dynamics. Additional studies are needed to confirm that map C could be a relevant brain electrical topographic neuromarker of cerebral adaptations to different modalities of physical exercise.

Some limitations—inherent to this kind of "in the field" scientific project—have to be enumerated. First, it must be kept in mind that the experiment was conducted under real conditions. Although the EEG recordings were acquired in a similar environment for every participant (e.g., same position and instructions; sound- and light-attenuated room), the postrace recordings were completed dozens of minutes after the participants had crossed the finished line at any time of day or night, regardless of the biological variation or circadian rhythms (i.e. Cajochen et al., 2002). Other methodological considerations must be considered (absence of control groups, drug use for pain management, dehydration, altitude, etc.). Consequently, the results should be interpreted cautiously. Second, it is well known that fatigue is a complex state. When induced by very long-lasting physical exercises (such as MUMs), fatigue could be explained by at least three main factors: physical engagement/fatigue, alertness/repetitiveness of the task (i.e., mental fatigue), and sleep deprivation. This study was not able to differentiate the relative impact of these main factors. However, we suggest that sleep deprivation is likely to be influential in the results obtained in this work. Third, we did not collect behavioural data, nor did we have time for individual interviews. Because the literature on runners' cognitive/attentional performance during ultramarathons is limited (see Hurdiel et al., 2018), implementing specific tests to investigate cognitive/attentional alterations would have been expected in the current study. However, one constraint we should face in this specific context was to reduce to minimum the burden of the runners (to be sure that they agree to start the experiment and come back at the end). By consequence, to facilitate the recruitment of participants, we decided to implement EEG sessions only. We are aware that the electrocortical signal can be modulated by several confounding factors like psychological/cognitive state but also, as mentioned above, by the moment of the day/night the EEG activity was recorded at the POST session. Indeed, Hurdiel and collaborators (2018) reported that the degree of cognitive deficits and self-reported sleepiness peaks vary according to the time-of day. Because our participants have crossed the finish line at any time (5 finishers between 8.00 am and 12.00 am, 5 finishers between 12.00 am and 10.00 pm, and 6 finishers between 10.00 pm and 8.00 am), we cannot exclude that the spontaneous electrocortical brain activity was not impacted by the circadian cycle in POST session. Nor we can exclude spindling activity – a specific oscillatory phenomenon of early stages of sleep – that could have emerged within the EEG traces after the race. However, considering that the two main types of sleep spindles are located in the frontal regions for the slow spindles (<13 Hz) and the centroparietal regions for the fast spindles (>13 Hz) (Schabus et al., 2007), we can reasonably assume that our findings were not significantly affected by these specific sleep EEG spindles. First, we did not find major changes in the frontal regions within the alpha frequency bands; second, we did not run frequency analyses above 12 Hz in the centroparietal region and third, the experimenters' role was to maintain the participant awaked to avoid him/her falling asleep. In addition, Hurdiel and collaborators (2018) reported that sleep management strategies during the race might alter psychological states and cognitive deficits. As we only collected the total hours of sleep but not the strategy itself, it is impossible to evaluate the impact of sleep management strategies on the electrocortical brain activity. Finally, other critical confounding factors (which were out of our control) might have affected the EEG data (e.g., medication for pain management, variation of altitude during the race, food consumption or dehydration).

In conclusion, the main findings of the current study revealed that changes in the power patterns of spontaneous electrical brain activity after ultraendurance footraces contrasts with changes in brain oscillatory activity induced by short endurance exercises. In addition, we found modulations in the RSNs related to bodily feedback collection and attentional processing, even though direct links between EEG microstates and brain networks need to be confirmed. Despite obvious methodological limitations that make difficult – if not impossible yet – the possibility by coaches or athletes to perform cerebral activity measurements without the assistance of researchers, some applications of the present findings are possible in terms of information/education of ultra-distance athletes. For example, education of the volunteers and/or the assistance crew may also limit the accidents of the runners due to cerebral impairments. The impact of high levels of sleep deprivation on the electrical brain activity and on the hyperactivation of the visual areas may also lead to appropriate sleeping strategies for limiting the cognitive performance deficit and the hallucinations (Hurdiel et al., 2018).

Declaration of Competing Interest

The authors declare that there is no conflict of interest.

Data Availability

The data used to support the findings of this study are available from the corresponding author upon request.

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References

Abeln, V., Schneider, S., Schiffer, T., Hollmann, W., & Strüder, H. K. (2015). Electrocortical and hemodynamic changes within the brain during incremental bicycle exercise in normoxia and hypoxia—a combined EEG/NIRS study. *Journal of Sports Science, 3*(3). https://doi.org/10.17265/2332-7839/2015.03.001

Antonova, E., Holding, M., Suen, H. C., Sumich, A., Maex, R., & Nehaniv, C. (2022). EEG microstates: Functional significance and short-term test-retest reliability. *Neuroimage: Reports, 2*(2), Article 100089. https://doi.org/10.1016/j.ynirp.2022.100089

Babiloni, C., Del Percio, C., Lizio, R., Noce, G., Lopez, S., Soricelli, A., … Stocchi, F. (2018). Functional cortical source connectivity of resting state electroencephalographic alpha rhythms shows similar abnormalities in patients with mild cognitive impairment due to Alzheimer's and Parkinson's diseases. *Clinical Neurophysiology, 129*(4), 766–782. https://doi.org/10.1016/j.clinph.2018.01.009

Babiloni, C., Marzano, N., Iacoboni, M., Infarinato, F., Aschieri, P., Buffo, P., … Del Percio, C. (2010). Resting state cortical rhythms in athletes: A high-resolution EEG study. *Brain Research Bulletin, 81*(1), 149–156. https://doi.org/10.1016/j.brainresbull.2009.10.014

Barry, R. J., Clarke, A. R., & Johnstone, S. J. (2011). Caffeine and opening the eyes have additive effects on resting arousal measures. *Clinical Neurophysiology, 122*(10), 2010–2015. https://doi.org/10.1016/j.clinph.2011.02.036

Barry, R. J., Clarke, A. R., Johnstone, S. J., Magee, C. A., & Rushby, J. A. (2007). EEG differences between eyes-closed and eyes-open resting conditions. *Clinical Neurophysiology, 118*(12), 2765–2773. https://doi.org/10.1016/j.clinph.2007.07.028

Bezzola, L., Mérillat, S., Gaser, C., & Jäncke, L. (2011). Training-Induced Neural Plasticity in Golf Novices. *The Journal of Neuroscience, 31*(35), 12444–12448. https://doi.org/10.1523/JNEUROSCI.1996-11.2011

Borghini, G., Astolfi, L., Vecchiato, G., Mattia, D., & Babiloni, F. (2014). Measuring neurophysiological signals in aircraft pilots and car drivers for the assessment of mental workload, fatigue and drowsiness. *Neuroscience & Biobehavioral Reviews, 44*, 58–75. https://doi.org/10.1016/j.neubiorev.2012.10.003

Bréchet, L., Brunet, D., Birot, G., Gruetter, R., Michel, C. M., & Jorge, J. (2019). Capturing the spatiotemporal dynamics of self-generated, task-initiated thoughts with EEG and fMRI. *NeuroImage, 194*, 82–92. https://doi.org/10.1016/j.neuroimage.2019.03.029

Britz, J., Van De Ville, D., & Michel, C. M. (2010). BOLD correlates of EEG topography reveal rapid resting-state network dynamics. *NeuroImage, 52*(4), 1162–1170. https://doi.org/10.1016/j.neuroimage.2010.02.052

Brodbeck, V., Kuhn, A., von Wegner, F., Morzelewski, A., Tagliazucchi, E., Borisov, S., … Laufs, H. (2012). EEG microstates of wakefulness and NREM sleep. *NeuroImage, 62*(3), 2129–2139. https://doi.org/10.1016/j.neuroimage.2012.05.060

Brümmer, V., Schneider, S., Abel, T., Vogt, T., & Strüder, H. K. (2011). Brain cortical activity is influenced by exercise mode and intensity. *Medicine & Science in Sports & Exercise, 43*(10), 1863–1872. https://doi.org/10.1249/MSS.0b013e3182172a6f

Brunet, D., Murray, M. M., & Michel, C. M. (2011). Spatiotemporal analysis of multichannel EEG: CARTOOL. *Computational Intelligence and Neuroscience*, 2011. https://doi.org/10.1155/2011/813870

Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network. *Annals of the New York Academy of Sciences, 1124*(1), 1–38. https://doi.org/10.1196/annals.1440.011

Cajochen, C., Wyatt, J. K., Czeisler, C. A., & Dijk, D. J. (2002). Separation of circadian and wake duration-dependent modulation of EEG activation during wakefulness. *Neuroscience, 114*(4), 1047–1060. https://doi.org/10.1016/S0306-4522(02)00209-9

Ciria, L. F., Luque-Casado, A., Sanabria, D., Holgado, D., Ivanov, P. C., & Perakakis, P. (2019). Oscillatory brain activity during acute exercise: Tonic and transient neural response to an oddball task. *Psychophysiology, 56*(5), Article e13326. https://doi.org/10.1111/psyp.13326

Ciria, L. F., Perakakis, P., Luque-Casado, A., & Sanabria, D. (2018). Physical exercise increases overall brain oscillatory activity but does not influence inhibitory control in young adults. *NeuroImage, 181*, 203–210. https://doi.org/10.1016/j.neuroimage.2018.07.009

Crabbe, J. B., & Dishman, R. K. (2004). Brain electrocortical activity during and after exercise: A quantitative synthesis. *Psychophysiology, 41*(4), 563–574. https://doi.org/10.1111/j.1469-8986.2004.00176.x

Craig. (2009). How do you feel — now? The anterior insula and human awareness. *Nature Reviews Neuroscience, 10*(1), 59–70. https://doi.org/10.1038/nrn2555

Craig, A., Tran, Y., Wijesuriya, N., & Nguyen, H. (2012). Regional brain wave activity changes associated with fatigue. *Psychophysiology, 49*(4), 574–582. https://doi.org/10.1111/j.1469-8986.2011.01329.x

Croce, P., Quercia, A., Costa, S., & Zappasodi, F. (2020). EEG microstates associated with intra- and inter-subject alpha variability. *Scientific Reports, 10*(1), 2469. https://doi.org/10.1038/s41598-020-58787-w

Custo, A., Van De Ville, D., Wells, W. M., Tomescu, M. I., Brunet, D., & Michel, C. M. (2017). Electroencephalographic Resting-State Networks: Source Localization of Microstates. *Brain Connectivity, 7*(10), 671–682. https://doi.org/10.1089/brain.2016.0476

Dahl, M. (2015). Weird Things Happen in the Minds of Ultramarathoners. The Cut. https://www.thecut.com/2015/11/weird-things-happen-in-the-minds-of-ultrarunners.html.

Dantzer, R., Heijnen, C. J., Kavelaars, A., Laye, S., & Capuron, L. (2014). The neuroimmune basis of fatigue. *Trends in Neurosciences, 37*(1), 39–46. https://doi.org/10.1016/j.tins.2013.10.003

Degache, F., Serain, E., Vernillo, G., Meyer, F., Falbriard, M., Savoldelli, A., … Millet, G. P. (2019). Postural control follows a bi-phasic alteration pattern during mountain ultra-marathon. *Frontiers in Physiology, 9. https://www. frontiersin. org/article/.* https://doi.org/10.3389/fphys.2018.01971

Degache, F., Zaen, J. V., Oehen, L., Guex, K., Trabucchi, P., & Millet, G. (2014). Alterations in postural control during the world's most challenging mountain ultra-marathon. *PLOS ONE, 9*(1), Article e84554. https://doi.org/10.1371/journal.pone.0084554

Del Percio, C., Derambure, P., Noce, G., Lizio, R., Bartrés-Faz, D., Blin, O., … PharmaCog Consortium. (2019). Sleep deprivation and Modafinil affect cortical sources of resting state electroencephalographic rhythms in healthy young adults. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology, 130*(9), 1488–1498. https://doi.org/10.1016/j.clinph.2019.06.007

Dietrich, A. (2006). Transient hypofrontality as a mechanism for the psychological effects of exercise. *Psychiatry Research, 145*(1), 79–83. https://doi.org/10.1016/j.psychres.2005.07.033

Dietrich, A., & Audiffren, M. (2011). The reticular-activating hypofrontality (RAH) model of acute exercise. *Neuroscience & Biobehavioral Reviews, 35*(6), 1305–1325. https://doi.org/10.1016/j.neubiorev.2011.02.001

Doppelmayr, M., Finkernagel, H., & Doppelmayr, H. I. (2005). Changes in cognitive performance during a 216 kilometer, extreme endurance footrace: a descriptive and prospective study. *Perceptual and Motor Skills, 100*(2), 473–487. https://doi.org/10.2466/pms.100.2.473-487

Doppelmayr, M., Sauseng, P., & Doppelmayr, H. (2007). Modifications in the human EEG during extralong physical activity. *Neurophysiology, 39*(1), 76–81. https://doi.org/10.1007/s11062-007-0011-z

Doppelmayr, M., Sauseng, P., Doppelmayr, H., & Mausz, I. (2012). Changes in EEG during Ultralong Running. *Journal of Human Performance in Extreme Environments, 10* (1). https://doi.org/10.7771/2327-2937.1047

Freund, W., Faust, S., Gaser, C., Grön, G., Birklein, F., Wunderlich, A. P., … Schütz, U. H. (2014). Regionally accentuated reversible brain grey matter reduction in ultra marathon runners detected by voxel-based morphometry. *BMC Sports Science, Medicine and Rehabilitation, 6*, 4. https://doi.org/10.1186/2052-1847-6-4

Glace, B., Murphy, C., & McHugh, M. (2002). Food and fluid intake and disturbances in gastrointestinal and mental function during an ultramarathon. *International Journal of Sport Nutrition and Exercise Metabolism, 12*(4), 414–427. https://doi.org/10.1123/ijsnem.12.4.414

Gogolla, N. (2017). The insular cortex. *Current Biology, 27*(12), R580–R586. https://doi.org/10.1016/j.cub.2017.05.010

Goodall, S., Twomey, R., & Amann, M. (2014). Acute and chronic hypoxia: Implications for cerebral function and exercise tolerance. *Fatigue. biomedicine, health & behavior, 2* (2), 73–92. https://doi.org/10.1080/21641846.2014.909963

Gutmann, B., Mierau, A., Hülsdünker, T., Hildebrand, C., Przyklenk, A., Hollmann, W., & Strüder, H. K. (2015). Effects of physical exercise on individual resting state EEG Alpha Peak Frequency. *Neural Plasticity*, 2015. https://doi.org/10.1155/2015/717312

Hilty, L., Langer, N., Pascual-Marqui, R., Boutellier, U., & Lutz, K. (2011). Fatigue-induced increase in intracortical communication between mid/anterior insular and motor cortex during cycling exercise. *European Journal of Neuroscience, 34*(12), 2035–2042. https://doi.org/10.1111/j.1460-9568.2011.07909.x

Hurdiel, R., Pezé, T., Daugherty, J., Girard, J., Poussel, M., Poletti, L., … Theunynck, D. (2015). Combined effects of sleep deprivation and strenuous exercise on cognitive performances during The North Face® Ultra Trail du Mont Blanc® (UTMB®). *Journal of Sports Sciences, 33*(7), 670–674. https://doi.org/10.1080/02640414.2014.960883

Hurdiel, R., Riedy, S. M., Millet, G. P., Mauvieux, B., Pezé, T., Elsworth-Edelsten, C., … Dupont, G. (2018). Cognitive performance and self-reported sleepiness are modulated by time-of-day during a mountain ultramarathon. *Research in Sports Medicine, 26*(4), 482–489. https://doi.org/10.1080/15438627.2018.1492401

Ishii, A., Tanaka, M., Shigihara, Y., Kanai, E., Funakura, M., & Watanabe, Y. (2013). Neural effects of prolonged mental fatigue: A magnetoencephalography study. *Brain Research, 1529*, 105–112. https://doi.org/10.1016/j.brainres.2013.07.022

Jeker, D., Falbriard, M., Vernillo, G., Meyer, F., Savoldelli, A., Degache, F., … Millet, G. P. (2020). Changes in spatio-temporal gait parameters and vertical speed during an extreme mountain ultra-marathon. *European Journal of Sport Science, 20* (10), 1339–1345. https://doi.org/10.1080/17461391.2020.1712480

Jung, T.-P., Makeig, S., Westerfield, M., Townsend, J., Courchesne, E., & Sejnowski, T. J. (2000). Removal of eye activity artifacts from visual event-related potentials in normal and clinical subjects. *Clinical Neurophysiology, 111*(10), 1745–1758. https://doi.org/10.1016/S1388-2457(00)00386-2

Kelly, A. M. C., & Garavan, H. (2005). Human functional neuroimaging of brain changes associated with practice. *Cerebral Cortex, 15*(8), 1089–1102. https://doi.org/10.1093/cercor/bhi005

Khanna, A., Pascual-Leone, A., Michel, C. M., & Farzan, F. (2015). Microstates in resting-state EEG: Current status and future directions. *Neuroscience & Biobehavioral Reviews, 49*, 105–113. https://doi.org/10.1016/j.neubiorev.2014.12.010

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition–timing hypothesis. *Brain Research Reviews, 53*(1), 63–88. https://doi.org/10.1016/j.brainresrev.2006.06.003

Knechtle, B., & Nikolaidis, P. T. (2018). Physiology and pathophysiology in ultra-marathon running. *Frontiers in Physiology*, 9. https://doi.org/10.3389/fphys.2018.00634

Koenig, T., Prichep, L., Lehmann, D., Sosa, P. V., Braeker, E., Kleinlogel, H., … John, E. R. (2002). Millisecond by Millisecond, Year by Year: Normative EEG Microstates and Developmental Stages. *NeuroImage, 16*(1), 41–48. https://doi.org/10.1006/nimg.2002.1070

Kraaier, V., Van Huffelen, A. C., & Wieneke, G. H. (1988). Quantitative EEG changes due to hypobaric hypoxia in normal subjects. *Electroencephalography and Clinical Neurophysiology, 69*(4), 303–312. https://doi.org/10.1016/0013-4694(88)90002-8

Kubitz, K. A., & Pothakos, K. (1997). Does aerobic exercise decrease brain activation? *Journal of Sport and Exercise Psychology*. https://doi.org/10.1123/jsep.19.3.291

Lahart, I. M., Lane, A. M., Hulton, A., Williams, K., Godfrey, R., Pedlar, C., … Whyte, G. P. (2013). Challenges in maintaining emotion regulation in a sleep and energy deprived state induced by the 4800km ultra-endurance bicycle race; the race across america (RAAM). *Journal of Sports Science & Medicine, 12*(3), 481–488.

Le Goff, C., Viallon, M., Kaux, J.-F., Andonian, P., Moulin, K., Seidel, L., … Millet, G. P. (2022). Kinetics of cardiac remodeling and fibrosis biomarkers during an extreme mountain ultramarathon. *Frontiers in Cardiovascular Medicine, 9*. https://www.frontiersin.org/article/10.3389/fcvm.2022.790551.

Leech, R., Braga, R., & Sharp, D. J. (2012). Echoes of the Brain within the Posterior Cingulate Cortex. *Journal of Neuroscience, 32*(1), 215–222. https://doi.org/10.1523/JNEUROSCI.3689-11.2012

Lehmann, D., Faber, P. L., Galderisi, S., Herrmann, W. M., Kinoshita, T., Koukkou, M., … Koenig, T. (2005). EEG microstate duration and syntax in acute, medication-naïve, first-episode schizophrenia: A multi-center study. *Psychiatry Research: Neuroimaging, 138*(2), 141–156. https://doi.org/10.1016/j.pscychresns.2004.05.007

Marzano, C., Moroni, F., Gorgoni, M., Nobili, L., Ferrara, M., & De Gennaro, L. (2013). How we fall asleep: Regional and temporal differences in electroencephalographic synchronization at sleep onset. *Sleep Medicine, 14*(11), 1112–1122. https://doi.org/10.1016/j.sleep.2013.05.021

Maufrais, C., Millet, G. P., Schuster, I., Rupp, T., & Nottin, S. (2016). Progressive and biphasic cardiac responses during extreme mountain ultramarathon. *American Journal of, 310*(10), H1340–H1348. https://doi.org/10.1152/ajpheart.00037.2016

McKellar, P., & Simpson, L. (1954). Between wakefulness and sleep: hypnagogic imagery. *British Journal of Psychology. General Section, 45*(4), 266–276. https://doi.org/10.1111/j.2044-8295.1954.tb01254.x

Menon, V. (2015). Salience Network. In *In Brain Mapping: An Encyclopedic Reference* (Vol. 2, pp. 597–611). Elsevier,.

Menon, V., & Uddin, L. Q. (2010). Saliency, switching, attention and control: A network model of insula function. *Brain structure & function, 214*(5–6), 655–667. https://doi.org/10.1007/s00429-010-0262-0

Merica, H., & Fortune, R. D. (2004). State transitions between wake and sleep, and within the ultradian cycle, with focus on the link to neuronal activity. *Sleep Medicine Reviews, 8*(6), 473–485. https://doi.org/10.1016/j.smrv.2004.06.006

Michel, C. M., & Koenig, T. (2018). EEG microstates as a tool for studying the temporal dynamics of whole-brain neuronal networks: A review. *NeuroImage, 180*, 577–593. https://doi.org/10.1016/j.neuroimage.2017.11.062

Michel, C. M., Koenig, T., Brandeis, D., Gianotti, L. R. R., & Wackermann, J. (2009). *Electrical Neuroimaging.* Cambridge University Press.

Millet, G. P., & Millet, G. Y. (2012). Ultramarathon is an outstanding model for the study of adaptive responses to extreme load and stress. *BMC Medicine, 10*(1), 77. https://doi.org/10.1186/1741-7015-10-77

Mojica, A.J. (2003). Within the Dreams, Reality, and Hallucinations of Ultra-Marathon Runners | Badwater. http://www.badwater.com/university/within-the-dreams-reality-and-hallucinations-of-ultra-marathon-runners/.

Nielsen, B., Hyldig, T., Bidstrup, F., González-Alonso, J., & Christoffersen, G. R. J. (2001). Brain activity and fatigue during prolonged exercise in the heat. *Pflügers Archiv, 442* (1), 41–48. https://doi.org/10.1007/s004240100515

Nieuwenhuis, S., Aston-Jones, G., & Cohen, J. D. (2005). Decision making, the P3, and the locus coeruleus—Norepinephrine system. *Psychological Bulletin, 131*(4), 510–532. https://doi.org/10.1037/0033-2909.131.4.510

Ozaki, H., Watanabe, S., & Suzuki, H. (1995). Topographic EEG changes due to hypobaric hypoxia at simulated high altitude. *Electroencephalography and Clinical Neurophysiology, 94*(5), 349–356. https://doi.org/10.1016/0013-4694(94)00311-8

Papadelis, C., Kourtidou-Papadeli, C., Bamidis, P. D., Maglaveras, N., & Pappas, K. (2007). The effect of hypobaric hypoxia on multichannel EEG signal complexity. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology, 118*(1), 31–52. https://doi.org/10.1016/j.clinph.2006.09.008.

Pascual-Leone, A., Amedi, A., Fregni, F., & Merabet, L. B. (2005). The plastic human brain cortex. *Annual Review of Neuroscience, 28*(1), 377–401. https://doi.org/10.1146/annurev.neuro.27.070203.144216

Pascual-Marqui, R. D. (2002). Standardized low-resolution brain electromagnetic tomography (sLORETA): technical details. *Methods & Findings in Experimental & Clinical Pharmacology, 24*(suppl. D), 5–12.

Pascual-Marqui, R. D., Michel, C. M., & Lehmann, D. (1995). Segmentation of brain electrical activity into microstates: Model estimation and validation. *IEEE Transactions on Biomedical Engineering, 42*(7), 658–665. https://doi.org/10.1109/10.391164

Paus, T., Koski, L., Caramanos, Z., & Westbury, C. (1998). Regional differences in the effects of task difficulty and motor output on blood flow response in the human anterior cingulate cortex: A review of 107 PET activation studies. *NeuroReport, 9*(9), R37.

Petruzzello, S. J., & Landers, D. M. (1994). State anxiety reduction and exercise: Does hemispheric activation reflect such changes? *Medicine & Science in Sports & Exercise, 26*(8), 1028–1035.

Petruzzello, S. J., & Tate, A. K. (1997). Brain activation, affect, and aerobic exercise: An examination of both state-independent and state-dependent relationships. *Psychophysiology, 34*(5), 527–533. https://doi.org/10.1111/j.1469-8986.1997.tb01739.x

Robertson, C. V., & Marino, F. E. (2016). A role for the prefrontal cortex in exercise tolerance and termination. *Journal of Applied Physiology, 120*(4), 464–466. https://doi.org/10.1152/japplphysiol.00363.2015

Saugy, J., Place, N., Millet, G. Y., Degache, F., Schena, F., & Millet, G. P. (2013). Alterations of neuromuscular function after the world's most challenging mountain ultra-marathon. *PLOS ONE, 8*(6), Article e65596. https://doi.org/10.1371/journal.pone.0065596

Savoldelli, A., Fornasiero, A., Trabucchi, P., Limonta, E., La Torre, A., Degache, F., Pellegrini, B., Millet, G.P., Vernillo, G., Schena, F. (2017). The Energetics during the World's Most Challenging Mountain Ultra-Marathon—A Case Study at the Tor des Geants®. Frontiers in Physiology, 8. https://www.frontiersin.org/article/10.3389/fphys.2017.01003.

Schabus, M., Dang-Vu, T. T., Albouy, G., Balteau, E., Boly, M., Carrier, J., … Maquet, P. (2007). Hemodynamic cerebral correlates of sleep spindles during human non-rapid eye movement sleep. *Proceedings of the National Academy of Sciences, 104*(32), 13164–13169. https://doi.org/10.1073/pnas.0703084104

Scheer, V. (2019). Participation trends of ultra endurance events. *Sports Medicine and Arthroscopy Review, 27*(1), 3. https://doi.org/10.1097/JSA.0000000000000198

Scheer, V., Basset, P., Giovanelli, N., Vernillo, G., Millet, G. P., & Costa, R. J. S. (2020). Defining off-road running: a position statement from the ultra sports science foundation. *International Journal of Sports Medicine, 41*(5), 275–284. https://doi.org/10.1055/a-1096-0980

Schneider, S., Askew, C. D., Diehl, J., Mierau, A., Kleinert, J., Abel, T., … Strüder, H. K. (2009). EEG activity and mood in health orientated runners after different exercise intensities. *Physiology & Behavior, 96*(4), 709–716. https://doi.org/10.1016/j.physbeh.2009.01.007

Seghier, M. L. (2013). The angular gyrus: multiple functions and multiple subdivisions. *The Neuroscientist, 19*(1), 43–61. https://doi.org/10.1177/1073858412440596

Seitzman, B. A., Abell, M., Bartley, S. C., Erickson, M. A., Bolbecker, A. R., & Hetrick, W. P. (2017). Cognitive manipulation of brain electric microstates. *NeuroImage, 146*, 533–543. https://doi.org/10.1016/j.neuroimage.2016.10.002

Sireteanu, R., Oertel, V., Mohr, H., Linden, D., & Singer, W. (2008). Graphical illustration and functional neuroimaging of visual hallucinations during prolonged blindfolding: a comparison to visual imagery. *Perception, 37*(12), 1805–1821. https://doi.org/10.1068/p6034

Smith, M. E., McEvoy, L. K., & Gevins, A. (2002). The impact of moderate sleep loss on neurophysiologic signals during working-memory task performance. *Sleep, 25*(7), 784–794.

Spring, J. N., Bourdillon, N., & Barral, J. (2018). Resting EEG microstates and autonomic heart rate variability do not return to baseline one hour after a submaximal exercise. *Frontiers in Neuroscience*, 12. https://doi.org/10.3389/fnins.2018.00460

Spring, J. N., Tomescu, M. I., & Barral, J. (2017). A single-bout of Endurance Exercise Modulates EEG Microstates Temporal Features. *Brain Topography*, 1–12. https://doi.org/10.1007/s10548-017-0570-2

Stock, C., Baum, M., Rosskopf, P., Schober, F., Weiss, M., & Liesen, H. (1996). Electroencephalogram activity, catecholamines, and lymphocyte subpopulations after resistance exercise and during regeneration. *European Journal of Applied Physiology and Occupational Physiology, 72*(3), 235–241.

Strijkstra, A. M., Beersma, D. G. M., Drayer, B., Halbesma, N., & Daan, S. (2003). Subjective sleepiness correlates negatively with global alpha (8–12 Hz) and positively with central frontal theta (4–8 Hz) frequencies in the human resting awake electroencephalogram. *Neuroscience Letters, 340*(1), 17–20. https://doi.org/10.1016/S0304-3940(03)00033-8

Tonacci, A., Mrakic-Sposta, S., Ujka, K., Sansone, F., Ferrisi, A., Giardini, G., … Pratali, L. (2017). Neurosensory and cognitive modifications in europe's toughest randoraid competition: the transpyrénéa extreme study. *Frontiers in Physiology*, 8. https://doi.org/10.3389/fphys.2017.00201

Vargas, N., & Marino, F. (2014). A neuroinflammatory model for acute fatigue during exercise. *Sports Medicine, 44*(11), 1479–1487. https://doi.org/10.1007/s40279-014-0232-4

Vargas, N., & Marino, F. (2018). Neuroinflammation, cortical activity, and fatiguing behaviour during self-paced exercise. *Pflügers Archiv - European Journal of Physiology, 470*(2), 413–426. https://doi.org/10.1007/s00424-017-2086-8

Vernillo, G., Rinaldo, N., Giorgi, A., Esposito, F., Trabucchi, P., Millet, G. P., & Schena, F. (2015). Changes in lung function during an extreme mountain ultramarathon. *Scandinavian Journal of Medicine & Science in Sports, 25*(4), e374–e380. https://doi.org/10.1111/sms.12325

Vernillo, G., Savoldelli, A., Zignoli, A., Trabucchi, P., Pellegrini, B., Millet, G. P., & Schena, F. (2014). Influence of the world's most challenging mountain ultra-marathon on energy cost and running mechanics. *European Journal of Applied Physiology, 114*(5), 929–939. https://doi.org/10.1007/s00421-014-2824-y

Vitiello, D., Degache, F., Saugy, J. J., Place, N., Schena, F., & Millet, G. P. (2015). The increase in hydric volume is associated to contractile impairment in the calf after the world's most extreme mountain ultra-marathon. *Extreme Physiology & Medicine, 4*(1), 18. https://doi.org/10.1186/s13728-015-0037-6

Xu, J., Pan, Y., Zhou, S., Zou, G., Liu, J., Su, Z., … Gao, J.-H. (2020). EEG microstates are correlated with brain functional networks during slow-wave sleep. *NeuroImage, 215*, Article 116786. https://doi.org/10.1016/j.neuroimage.2020.116786

Zanchi, D., Viallon, M., Le Goff, C., Millet, G. P., Giardini, G., Croisille, P., & Haller, S. (2017). Extreme mountain ultra-marathon leads to acute but transient increase in cerebral water diffusivity and plasma biomarkers levels changes. *Frontiers in Physiology, 7*. https://www.frontiersin.org/article/10.3389/fphys.2016.00664.

Zhao, J., Zhang, R., Yu, Q., & Zhang, J. (2016). Characteristics of EEG activity during high altitude hypoxia and lowland reoxygenation. *Brain Research, 1648*, 243–249. https://doi.org/10.1016/j.brainres.2016.07.013

Zmigrod, L., Garrison, J. R., Carr, J., & Simons, J. S. (2016). The neural mechanisms of hallucinations: A quantitative meta-analysis of neuroimaging studies. *Neuroscience & Biobehavioral Reviews, 69*, 113–123. https://doi.org/10.1016/j.neubiorev.2016.05.037