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Exercise practice associates with different brain rhythmic patterns during vigilance[1]

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ABSTRACT

Cardiovascular fitness has repeatedly been associated to enhanced cognitive and brain functioning, generally in the form of differences in reaction time and response accuracy, as well as in event-related potentials (ERPs) and blood-oxygen-level-dependent imaging while participants performed executive demanding tasks. However, the evidence regarding potential differences in oscillatory neural activity, an inherent characteristic of brain functioning, is scarce. To fill this gap, here, we extracted and analysed (using a data-driven exploratory approach) brain oscillatory activity, both tonic (overall electroencephalographic – EEG – oscillatory activity) and transient (event related spectral perturbation [ERSP] and inter-trial coherence [ITC]), from a previous published dataset (Luque-Casado et al. 2016), where we showed different behavioural and ERP patterns during a vigilance/sustained attention task as a function of cardiovascular fitness in young adults. The ERSP results of the current study revealed increased theta (4-8 Hz) and upper beta (20-40 Hz) power and reduced lower beta (14-20 Hz) suppression after the target stimulus presentation in the higher-fit group compared to their lower-fit peers, but these differences disappeared in the second part of the task. ITC results mimicked the ERSP pattern within theta (4-8 Hz), while no differences were observed for the remaining frequency bands. Interestingly, the overall time-dependent effect in transient oscillatory activity followed the reaction time pattern of results. The analysis of the overall EEG oscillatory (tonic) dynamics did not show significant differences between groups. In sum, cardiorespiratory fitness was related to a brain oscillatory differential response pattern over a wide range of the frequency spectrum and spatio-temporal distribution, which seems to underlie the positive relationship between aerobic fitness and behavioural performance in a sustained attention task. Future studies are warranted to study the causal nature (beyond mere association) of these findings.

1. Introduction

Cardiovascular fitness has been associated to improved cognitive and brain performance at all ages, indexed by individual differences in reaction time (RT) and response accuracy in tasks tapping (mainly) executive function [1], and in event-related brain potentials (ERPs) [2] or blood-oxygen-level-dependent imaging [3]. Much less is known, however, about potential differences as a function of fitness in oscillatory neural activity, an inherent characteristic of brain functioning. The current study aims at filling this gap in the literature by extracting and analyzing both the resting state and the task-dependent (transient) event-related spectral perturbations (ERSPs) and global (tonic) electroencephalographic (EEG) oscillatory activity from a dataset of one of our recent studies [4].

In Luque-Casado et al. (2016) [4], we showed that higher-fit young adults maintained larger P3 amplitude throughout a 60' version of the Psychomotor Vigilance Task (PVT) compared to lower-fit, who showed a reduction in the P3 magnitude over time. Additionally, a larger amplitude in the contingent negative variation (CNV) potential during the first half of the task was also shown by the higher-fit group. This ERP pattern mimicked that of the RT, which yielded shorter response time in the higher-fit group only in the first half of the experimental procedure. We concluded that higher fitness levels were related to electrophysiological activity suggestive of better ability to allocate attentional resources over time and a greater attentive preparatory state.

ERPs involve high temporal resolution and separated stimulus-

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locked potentials during task performance that offer relevant information about the mechanisms underlying cognitive functioning above and beyond that provided by behavioural measures. However, brain electrocortical activity is believed to be composed by diversified dynamic waveforms [5], and there is evidence pointing out that some ERP features may arise from changes in the dynamics of ongoing neural oscillations [6,7]. This evidence presumes a strong dependency between neural oscillations and ERPs, arguing that ERPs are generated, at least in part, by a reset of ongoing oscillations [7]. Thus, brain oscillations play an important functional role and interact with the ERPs and, consequently, evidence from ongoing brain rhythms analysis could be transferred to findings of ERP research and vice versa [6]. Additionally, the timing and direction of a change in brain oscillatory activity induced by an event or stimulus at a specific frequency band functionally reflect rhythmic changes in excitation of a population of neurons that reflect ongoing sensory, motor and/or cognitive processes [5,8]. ERSP analysis represent an excellent index of neural communication through which the dynamics of the power of frequency-specific oscillations are quantified and these spatiotemporal dynamics are examined providing links to associative and integrative brain functions [9].

In the search for brain function biomarkers of the fitness-related improvements in cognition, the ERSP approach is therefore an attractive proposition as it may provide complementary information to that of the ERPs. Crucially, as the ERSP contains contributions from both phase-locked and non-phase-locked oscillations, the contributions of non-phase-locked induced oscillations offer additional discriminatory information as an alternative interpretation for cortical activity while performing a cognitive task [10].

Even though the analysis of brain oscillations could further elucidate the underlying processes of the fitness-related improvements in cognition, no study so far has explored the relationship between sustained attention performance and aerobic fitness by using this approach. This is particularly noteworthy since brain oscillatory activity has been shown to be a key mechanism supporting sustained attention performance [11]. In fact, time-related variations and deterioration in attention are strongly associated with specific changes in oscillatory EEG features [12]. Therefore, investigating cortical oscillations can be of both great practical significance and substantial theoretical interest in this area of research by leading to a deeper understanding of the exercise and cognition relationship in general, and sustained attention in particular.

Here, we stand to provide novel evidence of the relationship between aerobic fitness and neural oscillatory patterns of young adults in a prolonged sustained attention task. To this aim, we extracted and analysed the resting state, global EEG task-related and transient oscillatory activity (ERSPs) from the dataset of our previous ERP study [4]. Additionally, following on the sound suggestions of an anonymous reviewer, we computed inter-trial coherence (ITC). Based on the spectral range and spatiotemporal heterogeneity of the oscillatory mechanisms underlying the performance in sustained attention [11], and given that we did not have clear *a priori* hypotheses regarding fitness as a prone factor to modulate neural oscillations in vigilance contexts, we took an exploratory approach (cf. Wagenmakers et al. [13]), with a bottom-up methodology by employing a stepwise cluster-based analysis.

2. Material and methods

Details on materials and methods are reported in the original study [4], but we include them here again for the sake of clarity and completeness.

2.1. Participants

We recruited fifty young male adults from a larger pool of eighty-nine undergraduate students and members of local triathlon clubs, which were assigned to a higher-fit ($N = 25$) and lower-fit group ($N = 25$) based on the inclusion criteria of reporting at least 8 hours of training per week or less than 2 hours, respectively. Their fitness level was confirmed by a submaximal cardiorespiratory fitness test. The reader will note a difference in the number of participants included in the behavioural and EEG data analysis regarding our previous report [4]. Here, based on the EEG data processing, only one participant from the higher-fit group was excluded from the analyses (see *EEG recordings and data reduction section*). Data from the remaining 49 participants are reported (see Table 1).

Table 1
Mean and 95% Confidence Interval (CI) of descriptive, fitness and behavioural data for the higher-fit and lower-fit groups.

		Higher-fit	Lower-fit
Anthropometrical characteristics			
Sample size		24	25
Age (years)		23 [21, 24]	23 [22, 24]
Height (m)		1.77 [1.75, 1.79]	1.78 [1.76, 1.81]
Weight (kg)		69.3 [66.9, 71.6]	76.7 [69.4, 84.0]
Body Mass Index ($kg \cdot (m^2)^{-1}$)		22.2 [21.5, 22.9]	24.0 [22.2, 25.7]
Incremental test parameters			
Time to VAT (s)*		1270 [1163.3, 1377.2]	493 [433.3, 551.9]
VO_2 ($mL \cdot min^{-1} \cdot kg^{-1}$) at VAT*		43.3 [40.0, 46.6]	19.5 [17.5, 21.5]
Relative power output at VAT ($W \cdot kg^{-1}$)*		3.41 [3.10, 3.72]	1.40 [1.23, 1.56]
Psychomotor Vigilance Task (PVT)			
Mean RTs (ms)	Block 1	269.4 [259.4, 279.3]	279.3 [264.4, 294.2]
	Block 2	295.3 [282.2, 308.4]	294.9 [277.2, 312.6]

* Indicates statistically significant differences between groups ($p < 0.001$); VAT (ventilatory anaerobic threshold).

All participants met the inclusion criteria of reporting normal or corrected to normal vision, reported no neurological, cardiovascular or musculoskeletal disorders and were taking no medication. Participants were required to maintain regular sleep-wake cycle for at least one day before the experimental session and to abstain from stimulating beverages or any intense physical activity 24 hours before the laboratory visit. Table 1 presents the anthropometrical characteristics and descriptive data of the sample. The experiment was conducted according to the ethical requirements of the University of Granada ethical committee and in compliance with the Helsinki Declaration. All participants were informed about their right to leave the experiment at any time and gave written informed consent prior to their inclusion in the study.

2.2. Procedure

Upon arrival to the laboratory, participants were seated in front of a computer in a dimly illuminated, sound-attenuated room with a Faraday cage. All participants received verbal and written information about the experiment and they were prepared for electrophysiological measurement. Eyes-open resting state EEG signal was recorded for 5 min in which participants were asked to stay as relaxed as possible and to view a blank wall in front of them. After a brief training session, participants were instructed to complete a 60' version of the PVT. We used a PC with a 19'' monitor and E-Prime software (Psychology Software Tools, Pittsburgh, PA, USA) to control the stimulus presentation, response collection, and to generate and send triggers indicating the condition of each trial for offline sorting, reduction, and analysis of EEG and behavioural data. The centre of the PC screen was situated at eye level approximately 60 cm from the head of the participants. A PC keyboard was used to record behavioural responses.

After PVT completion, all participants performed a submaximal cycle ergometer cardiorespiratory fitness test to evaluate their fitness level (see Table 1). This test was performed after the PVT in order to avoid the influence of physical effort on cognitive performance [14]. The entire experimental session lasted 2 h approximately.

2.3. Submaximal cardiorespiratory fitness test

Prior to the start of the fitness test, descriptive anthropometric parameters of weight, height and body mass index (BMI) were obtained for each participant (see Table 1). Then, all participants were fitted with a Polar RS800 CX monitor (Polar Electro Öy, Kempele, Finland) to record their heart rate (HR) during the incremental exercise test. We used a ViaSprint 150 P cycle ergometer (Ergoline GmbH, Germany) to induce physical effort and to obtain power values and a JAEGER Master Screen gas analyser (CareFusion GmbH, Germany) to provide a measure of gas exchange during the test.

The incremental effort test started with a 3 minutes warm-up at 30 Watts (W), with the power output increasing 10 W every minute. During this warm-up period, each participant set his preferred cadence (between 60-90 rev • min^{-1}) and was asked to maintain this cadence throughout the protocol. The test began at 60 W and was followed by an incremental protocol with the power load increasing 30 W every 3 minutes. Workload increased progressively during the third minute of each step (5 W every 10 seconds [s]); therefore, each step of the incremental protocol consisted of 2 minutes of stabilized load and 1 minute of progressive load increase. The oxygen uptake (VO2 ml • min^{-1} • kg^{-1}), respiratory exchange ratio (RER; i.e., CO_2 production • O_2 $consumption^{-1}$), relative load (W • Kg^{-1}), heart rate (bpm) and time of the test (s) were continuously recorded during the entire incremental test.

We used the ventilatory anaerobic threshold (VAT) as a reference to determine the fitness level of the participants (see Table 1). VAT is considered to be a sensitive measure for evaluating aerobic fitness and cardiorespiratory endurance performance [17,18] and was defined as the VO_2 at the power load in which RER exceeded the cut-off value of 1.0 [19,20]. The researcher knew that the participant had reached his VAT when the RER was equal to 1.00 and did not drop below that level during the 2 minutes constant load period or during the next load step, never reaching the 1.1 RER. The submaximal cardiorespiratory fitness test ended once the VAT was reached.

2.4. The psychomotor vigilance task (PVT)

The procedure of the PVT was based on the original version [15]. This task was designed to measure vigilance by recording participants' reaction times (RTs) to visual stimuli that occur at random inter-stimulus intervals [15,16]. Each trial began with the presentation of a blank screen in a black background for 2000 ms and subsequently, an empty red circumference (i.e., cue stimulus, 6.68° × 7.82° of visual angle at a viewing distance of 60 cm) appeared in a black background. Later, in a random time interval (between 2000 and 10000 ms), the circumference was filled all at once in a red colour (i.e., target stimulus). Participants were instructed to respond as fast as they could once they had detected the presentation of the filled circle. The filled circle was presented for 500 ms and the participants had a maximum of 1500 ms to respond. They had to respond with the index finger of their dominant hand by pressing the space bar on the keyboard. A RT visual feedback message was displayed for 300 ms after response, except in case of an anticipated response ("*wait for the target*") or if no response was made within 1000 ms after target offset ("*you did not answer*"). Following the feedback message, the next trial began. The task lasted 60 minutes and the mean number of trials per participant was 422 ± 6.5.

2.5. Electroencephalogram (EEG) recordings and data reduction

EEG data were recorded at 1024 Hz using a 64-channel BioSemi Active Two system (Biosemi, Amsterdam, Netherlands) with active scalp Ag/AgCl electrodes arranged according to the international standard 10–20 system. The common mode sense (CMS) and driven right leg (DRL) electrodes served as the ground, and all scalp electrodes were referenced to the CMS during recording. Electrode impedances were kept below 10 kΩ. Participants were instructed to avoid eye movements, blinking, and body movements as much as possible, and to keep their gaze on the centre of the screen during task performance.

We used a combination of custom Matlab scripts (Matlab 2013a, Mathworks Inc.), the EEGLAB toolbox [21] (version 13.6.5b) and Fieldtrip toolbox [22] for processing and analysing EEG data. Continuous data were down-sampled to 256 Hz, re-referenced to the average of all electrodes (average common reference) and bandpass filtered offline from 1 to 40 Hz using a zero-phase Hamming-windowed sinc Finite Impulse Response (FIR) filter (-6dB cut-off frequency and default mode filter order/transition bandwidth implementation; EEGLAB toolbox). Electrodes presenting abnormal power spectrum were identified via visual inspection and replaced by spherical interpolation. Independent Component Analysis (ICA) [21] was used to identify and remove EEG components reflecting eye blinks. The ocular ICA components were removed in a systematic way for all participants to avoid any bias across the groups. One participant in the higher-fit group presented abnormal spectra epochs in 50% of the trials and was excluded from the analyses in order to ensure optimal signal-to-noise ratio.

Spectral power analysis. Processed EEG data segments from each experimental condition (i.e., resting state and task-related spectral power during cognitive performance) were subsequently segmented to 1-s epochs. Spectral decomposition for each epoch was computed by using Fast Fourier Transform (FFT) applying a symmetric Hamming window and the obtained power values were averaged across experimental conditions. In addition to the absolute power (AP) across experimental condition, the relative power was also examined. To this end, the percentage change in absolute spectral power from resting state to task-related EEG during cognitive performance (Δ) was calculated for each individual frequency from 1 to 40 Hz as follow: Relative power (Δ) = ((AP during task – AP resting state) • AP resting $state^{-1}$) •100.

Time-frequency analysis. Task-evoked spectral EEG activity was assessed by computing event-related spectral perturbations in epochs extending from –1000 ms to 2000 ms time-locked to stimulus onset for frequencies between 4 and 40 Hz. Separate epochs were constructed for cues and targets stimuli. Spectral decomposition was performed using sinusoidal wavelets with 3 cycles at the lowest frequency and increasing by a factor of 0.8 with increasing frequency. Power values were normalised with respect to a −300 ms to 0 ms pre-stimulus baseline and transformed into the decibel scale (10•log10 of the signal).

The phase spectral properties were also explored by calculating the ITC as a secondary control analysis in order to provide insight into the interplay of the induced stimulus-related power increase (or decrease) and phase synchronization of ongoing activity [23–25]. ITC measures the consistency across trials of EEG spectral phase at each frequency and latency window. The ITC measurement takes values from 0 (no coupling) to 1 (complete phase locking) across trials [21].

Behavioural analysis. The behavioural data analyses were performed on the overall participants' mean RTs. Anticipations (i.e., responses prior to the target presentation) and omissions (if no response was given within 1000 ms after target offset) can be taken as response errors, but the ratio of this type of responses was extremely low and did not allow obtaining a reliable index to be properly evaluated. Thus, anticipations (1.33%), trials with RTs < 100 ms (0.03%) and omissions (0.27%) were finally discarded from both behavioural and EEG analyses [16].

2.6. Design and statistical analysis

Behavioural and participants' fitness and anthropometrical data. The behavioural data were analysed through repeated measures analysis of variance (ANOVA) with the between-participants factor of Group (higher-fit, lower-fit) and the within-participants factor of Block (B1, B2). The effect sizes were reported by partial eta-squared ($\eta_{partial}^2$). A *t*-

test for independent samples was applied to analyse the participants' fitness and anthropometrical data.

Resting state and task-related spectral power during cognitive performance. We used a stepwise cluster-based non-parametric permutation analysis [26] (Fieldtrip toolbox) without prior assumptions on any frequency range or region of interest. The algorithm performed a two-tailed *t*-test for independent samples on all individual *electrodes (64)* X *frequencies (1Hz bins from 1 to 40Hz)* pairs and clustered samples with positive and negative *t*-values that exceeded a threshold (i.e., $p < 0.025$) based on spatial and spectral adjacency. Cluster-level statistics were then calculated by taking the sum of the *t*-values within each cluster. The data points from the two datasets were randomly shuffled and the maximum cluster-level statistic for these new shuffled datasets was calculated. The above procedure was repeated 4000 times to estimate the distribution of maximal cluster-level statistics obtained by chance. The proportion of random partitions that resulted in a larger test statistic than the original one determined the two-tailed Monte-Carlo p-value. A *p*-value of the original cluster statistic smaller than the critical Monte-Carlo *p*-value indicated significant differences between the two datasets.

Spectral power main effect of Group (higher-fit *vs*. lower-fit) was tested for significance at resting state period. For task-related spectral power during cognitive performance, we split the analysis into two temporal blocks (30 min each) to explore a possible time-on-task effect on the spectral power. Note that the number of blocks of the PVT in the analysis was reduced to two in order to simplify the design and increase the signal-to-noise ratio of the cluster-based EEG analysis. We therefore ended up with a 2 (Group: higher-fit, lower-fit) x 2 (Block: B1, B2) design. Firstly, we tested the interaction Group X Block by applying the permutation test to the spectral power (SP) difference SP_{B2}-SP_{B1}. The main effect of Group was tested by applying the test to the averaged data set $SP_{B1B2} = ½ \cdot (SP_{B1} + SP_{B2})$. Since the aim of this study was to identify differences as a function of aerobic fitness of the participants, only significant main effects and interactions for the factor Group are reported. These comparisons were performed both for absolute and relative power datasets for each electrode and frequency bin of 1Hz without *a priori* assumptions on the region of interest or frequency range.

Time-frequency analysis. ERSP and ITC during task performance were also obtained for cue and target stimulus, respectively. Again, we followed the above-mentioned 2 (Group: higher-fit, lower-fit) x 2 (Block: B1, B2) factorial design and statistical approach. Significant main effects and interactions for the factor Group were also analysed by applying the cluster-based non-parametric permutation test. In order to reduce the possibility that the type II error rate was inflated by multiple comparisons correction, we set an *a priori* criteria of averaging power and phase values across four previously defined frequency bands: theta (4-8 Hz), alpha (8-14 Hz), lower beta (14-20 Hz) and upper beta (20-40 Hz). Additionally, to avoid an overlap with behavioural responses, we also limited the time windows of interest to the first 300 ms after the target onset (based on average behavioural response times). Note that due to a methodological limitation with the spectral decomposition algorithm, the time window of interest for the cue stimulus was limited to the first 1500ms. In this case, the algorithm performed a two-tailed t-test for independent samples on all individual *electrodes (64)* X *time point (cue: 0-1500ms; target 0-300ms)* pairs and clustered samples with positive and negative *t*-values that exceeded a threshold (i.e., $p < 0.025$) based on spatial and temporal adjacency. These comparisons were performed both for cue and target datasets for each electrode and time point without *a priori* assumptions on the spatial or temporal region of interest.

3. Results

Descriptive and fitness data. The t-tests for independent samples revealed significant differences between groups in the VO_2 ($mL \cdot min^{-1} \cdot kg^{-1}$) at VAT, $t(47) = 11.93$, $p < 0.001$, relative power output ($W \cdot kg^{-1}$) at VAT, $t(47) = 11.29$, $p < 0.001$, and time to reach VAT (s), $t(47) = 12.34$, $p < 0.001$. All data showed evidence of the difference in fitness level between groups (see Table 1). There were no statistically significant differences between groups in any of the remaining descriptive or anthropometrical data, i.e., age ($p = 0.61$), height ($p = 0.38$), weight ($p = 0.08$) or body mass index ($p = 0.09$).

Behavioural results. A repeated-measures ANOVA with the between-participants factor of Group (higher-fit, lower-fit) and the within-participants factor of Block (B1, B2) was conducted on participants' mean RTs. The main effect of Group was not significant ($F < 1$). By contrast, both the main effect of Block, $F(1,47) = 68.22$, $p < 0.001$, $\eta_p^2 = .59$, and the interaction between Group and Block reached statistical significance, $F(1,47) = 4.27$, $p = 0.04$, $\eta_p^2 = .08$. This significant interaction was depicted by shorter RTs in the first 30 min of the task in the higher-fit compared to the lower-fit group, while both groups matched poor performance in the second half of the task. In any case, the post-hoc comparisons did not reach statistical significance (both $ps \geq 0.25$). Mean RTs and 95% confidence intervals (CI) are reported in Table 1. The statistical results presented here do not fully correspond with those reported in our previous article [4]. It is important to note that here we maintained 49 out of 50 participants after the EEG data processing and we substantially reduced the number of temporal blocks in order to find the proper balance by increasing the signal-to-noise ratio for the EEG spectral analysis. In any case, the general pattern of behavioural outcomes is the same that was in turn supported by the EEG analysis.

Resting state and task-related spectral power during cognitive performance. Resting state absolute spectral power analyses did not detect any significant cluster for the main effect of Group ($p = 0.22$). Similarly, the main effect of Group and the interaction between Group and Block were not significant for task-related spectral power during cognitive performance (both $ps \geq .23$). Regarding the relative power analysis, there was a greater rest-to-task increase of high frequencies EEG power (from 23 to 39 Hz) in higher-fit (8.06 %) compared to lower-fit participants (3.09 %; see Fig. 1 for descriptive spectra), although it did not reach statistical significance (6 electrodes occipital cluster; $p = 0.08$). There were no significant clusters for the interaction between Group and Block (all $ps \geq 0.28$).

Time-frequency analysis. Cue-related spectral perturbation analysis across the different frequency bands did not reveal any significant cluster for either the main effect of Group or the Group and Block interaction (all $ps \geq 0.15$; see Fig. 2).

Target-related analysis for the main effects of Group did not reveal significant clusters for any of the frequency bands (all $ps \geq 0.38$). By contrast, the analysis of the interaction between Group and Block showed statistically significant differences within the theta, lower and upper beta frequency bands, although it did not reach significance for the alpha band ($p = .18$). The theta band analysis exhibited a 19-electrodes significant cluster from 0 to 156 ms after the target onset ($p = 0.02$). The higher-fit group showed a greater spectral power in block 1 compared to lower-fit group, although there were no group differences in block 2 (see Fig. 3). The lower beta band analysis revealed a 32-electrodes cluster distributed from 145 to 300 ms ($p < 0.01$). The higher-fit group showed no lower beta suppression until 300ms after the target appearance, unlike the early suppression showed by the lower-fit group in the first part of the task. However, both groups showed a similar early suppression pattern in block 2 (see Fig. 3). Finally, the upper beta band analysis also yielded a 39-electrodes significant cluster ranging from 156 to 300 ms after the target onset ($p < 0.01$). This interaction was depicted by a greater spectral power in block 1 in higher-fit compared to lower-fit participants, while the difference disappeared in the second part of the task (see Fig. 3).

ITC analysis only depicted statistically significant differences for the target-related interaction between Group and Block within the theta frequency band. Specifically, the theta band analysis exhibited two significant clusters (15-electrodes and 18-electrodes) within an

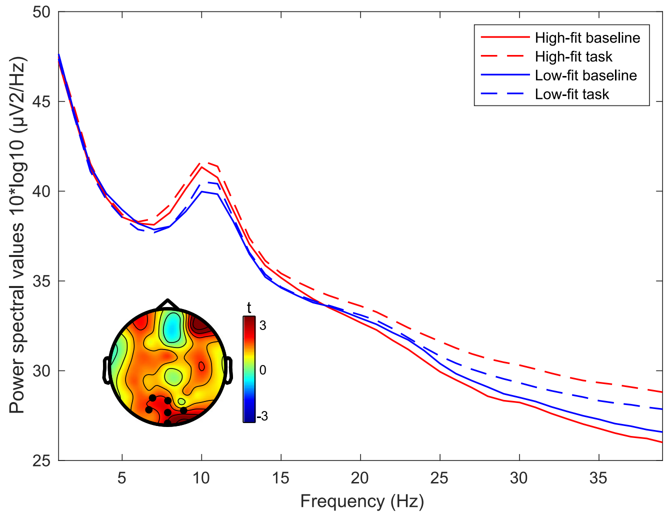

Fig. 1. Resting state and task-related spectral power during cognitive performance as a function of Group. Solid lines represent the resting state absolute spectral power and dashed lines represent the task-related spectral power during cognitive performance for higher-fit (red) and lower-fit (blue) participants. The x-axis represents the frequencies across the spectrum and the y-axis the power values for each individual frequency. The electrode sites within the occipital cluster in high frequencies power (23-39 Hz) rest-to-task increase in higher-fit (8.06 %) and lower-fit participants (3.09 %) are represented. *T*-test values distribution from contrasting the between-groups power differences in rest-to-task increase across all individual electrodes and frequencies are represented in the topographic colorbar plot (bottom-left). Note that this cluster did not reach statistical significance ($p = 0.08$) and is represented only for a descriptive purpose. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

identical time range (from 0 to 133 ms) after the target onset (both $ps \leq 0.02$). In both clusters, the higher-fit group showed a greater ITC values in block 1 compared to lower-fit group, although there were no group differences in block 2 (see Fig. 4). There were no significant clusters for either the main effect of Group or the Group and Block interaction across the remaining frequency bands for both cue- and target-related analyses (all $ps \geq .10$).

4. Discussion

In the present study, we took an exploratory bottom-up approach to describe, for the first time, the relationship between cardiovascular fitness and neural oscillatory patterns in young adults in a prolonged sustained attention task. To this end, we extracted and analysed the ERSPs and overall EEG oscillatory dynamics of a set of data from our laboratory [4] comparing performance of two groups of participants (i.e., higher-fit and lower-fit) in a 60' version of the PVT.

The results of the resting state and task-related (overall) spectral power during cognitive performance did not show any significant result. This result contradicts the scarce previous evidence pointing to a selective association between aerobic fitness and tonic EEG overall dynamics [27,28]. The ERSP analysis did show significant differences as a function of cardiovascular fitness, such that higher-fit group showed an increased theta and upper beta power, as well as reduced lower beta suppression after the target presentation with respect to their lower-fit counterparts in the first part of the task, but these differences disappeared in the second block. The reader will note that the modulation of the ERSP by the time-on-task paralleled the reaction time pattern reported here and in Luque-Casado et al. [4], with higher-fit participants outperforming lower-fit participants in terms of reaction time to the target stimulus in the first half of the PVT.

The joint analysis of ERSP and ITC depicted a coincident response within the theta frequency band, in which higher-fit showed greater power and inter-trial coherence with respect to lower-fit, although limited to the first block of the task. In light of the evidence showing that ERPs could arise from partial phase synchronization of ongoing activity combined with a stimulus-related change in EEG power [24,25,29], it is reasonable to argue that activity within the theta band could be contributing, at least in part, to the genesis of the P3 component described in our previous report [4]. Nevertheless, the P3 and frontal midline theta power and inter-trial coherence have proven to be key neural signatures that, while underlying vigilance performance synergistically, seem to reflect activity of different anatomical substrates distinctively involved in attentional stability and flexibility procedures [30]. Fronto-medial theta power has been linked to cognitive monitoring and control processes [31–33], thought to be crucial for sustained attention [11,32]. In a similar vein, trial-by-trial phase consistency of the theta oscillation has proven to be critical for the ability

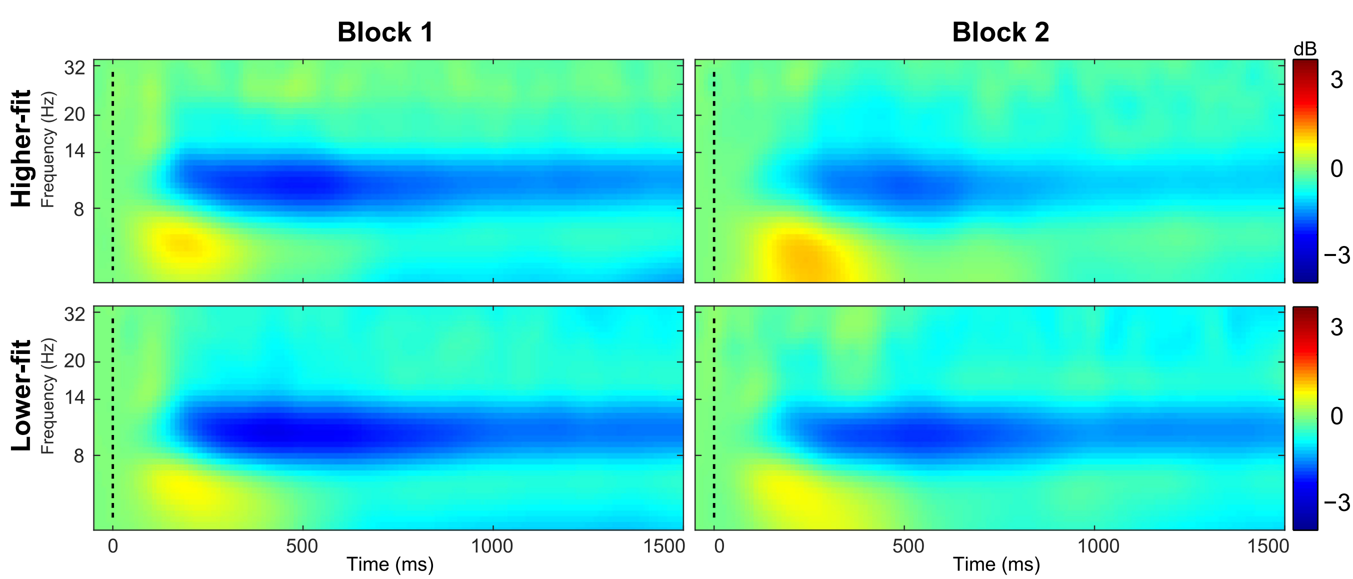

Fig. 2. Representation of the event-related spectral perturbation (ERSP) after the cue stimulus appearance as a function of Group and Block. Time-frequency graphs averaging all electrodes as a function of Group (top: higher-fit; bottom: lower-fit) and Block (left: block 1; right: block 2); Colorbar represents power values in decibels (dB), *y*-axis represents frequency in hertz (Hz) and *x*-axis represents time point in milliseconds (ms). Time zero represents the cue stimulus appearance. Note that no significant clusters were found for either the main effect of Group or the Group and Block interaction across the different frequency bands.

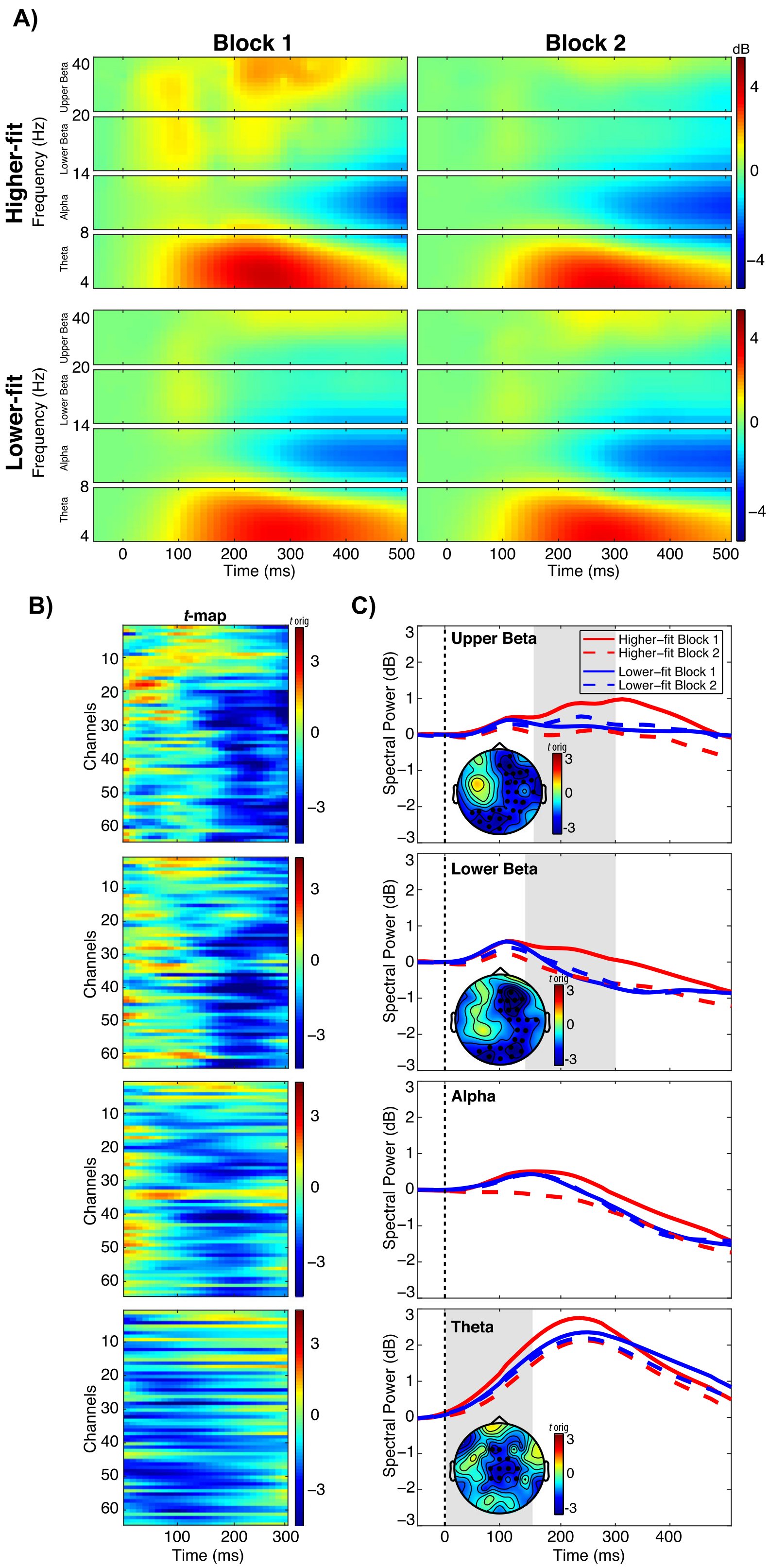

Fig. 3. Representation of the event-related spectral perturbation (ERSP) after the target stimulus appearance and the significant clusters in theta (4-8 Hz), lower beta (14-20 Hz) and upper beta band (20-40 Hz) as a function of Group and Block. A) Time-frequency graphs at electrode sites included within the significant cluster in each frequency band as a function of Group (top: higher-fit; bottom: lower-fit) and Block (left: block 1; right: block 2); Colorbar represents power values in decibels (dB), *y*-axis represents frequency in hertz (Hz) and *x*-axis represents time point in milliseconds (ms). Time zero represents the target stimulus appearance; B) Descriptive representation of *t*-test values distribution (colorbar) of the Group and Block interaction evaluated by the between-groups contrast (i.e., higher-fit vs. lower-fit) of the Block differences (i.e., block 2 - block 1) across all individual electrodes (*y*-axis) and time point (*x*-axis) pairs. Note that samples of *t*-values that exceeded the fixed threshold ($p < 0.025$) were clustered based on spatial and temporal adjacency. The significant clusters are represented in graph C; C) Grand average of target-related spectral perturbation as a function of Group (red lines: higher-fit; blue lines: lower-fit) and Block (solid lines: block 1; dashed lines: block 2) after the target onset. The shaded area represents the latency range where significant interactions between Group and Block were found. The electrode sites included in the significant cluster are highlighted in black in the topographic *t*-values plot. *Y*-axis represents the power values (dB), *x*-axis represents the time point (ms) and the topography colorbar represents *t*-values. No significant cluster was found within the alpha band and the topographic *t*-values plot was not represented in this case. Alternatively, an average of all electrodes is plotted in graph C for a descriptive purpose. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

to maintain attentional focus from moment to moment [30], which could be leading to a more stable and efficient response [34]. In any case, although this combined ERSP and ITC analysis gives a deeper insight to understanding of neural responses, compelling neurophysiological evidence for a clear dissociation between biological processes underlying phase-locked versus non-phase-locked activity is still needed [23,35,36] and caution should therefore be exercised around any interpretation.

ERSP in higher-fit participants also showed no suppression in lower beta and exhibited an increased power in upper beta band with respect to their lower-fit peers during the execution of the first part of the task. Again, in the second part of the task, the fitness-related differences

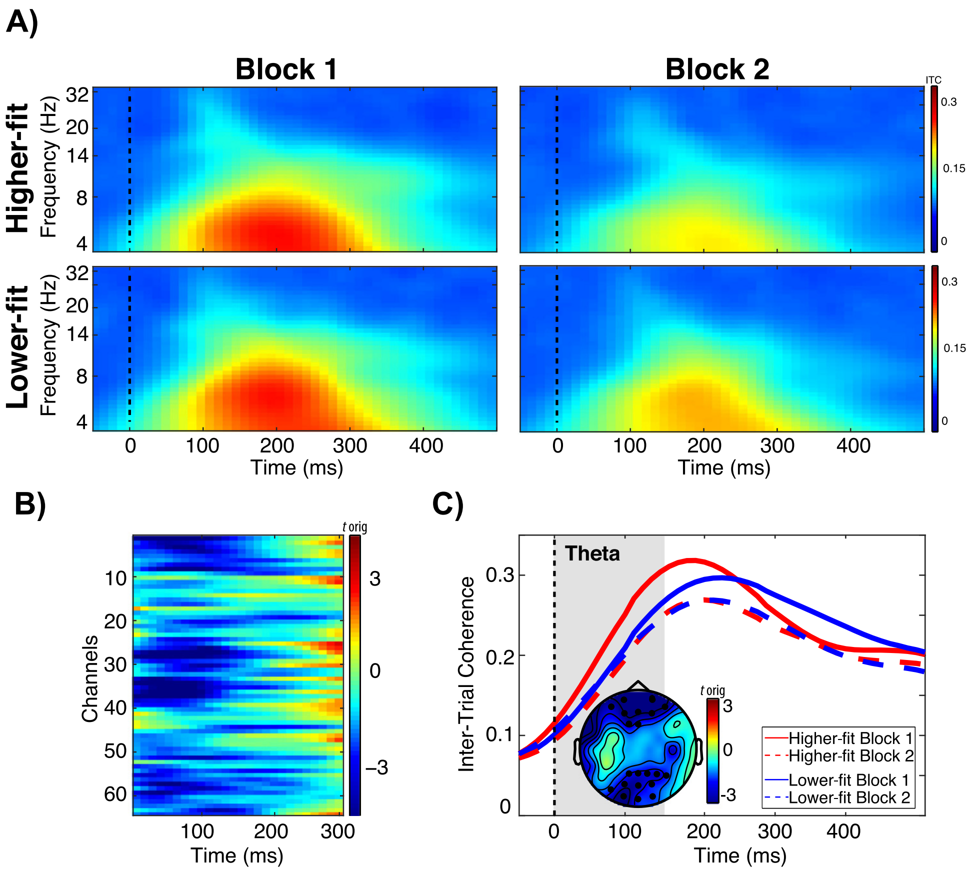

Fig. 4. Representation of the inter-trial coherence (ITC) value after the target stimulus appearance and the significant clusters in theta band (4-8 Hz) as a function of Group and Block. A) Time-frequency graphs at electrode sites included within the significant clusters as a function of Group (top: higher-fit; bottom: lower-fit) and Block (left: block 1; right: block 2); Colorbar represents ITC values ranging from a minimum of 0 (no coupling) to a maximum of 1 (complete phase locking) across trials, *y*-axis represents frequency in hertz (Hz) and *x*-axis represents time point in milliseconds (ms). Time zero represents the target stimulus appearance; B) Descriptive representation of *t*-test values distribution (colorbar) of the Group and Block interaction evaluated by the between-groups contrast (i.e., higher-fit vs. lower-fit) of the Block differences (i.e., block 2 - block 1) across all individual electrodes (*y*-axis) and time point (*x*-axis) pairs. Samples of *t*-values that exceeded the fixed threshold ($p<0.025$) were clustered based on spatial and temporal adjacency. The significant clusters are represented in graph C; C) Grand average of target-related ITC values as a function of Group (red lines: higher-fit; blue lines: lower-fit) and Block (solid lines: block 1; dashed lines: block 2) after the target onset. The shaded area represents the latency range where significant interaction between Group and Block was found. The electrode sites included within the significant clusters are highlighted in black in the topographic t-values plot. *Y*-axis represents the represents ITC values, *x*-axis represents the time point (ms) and the topography colorbar represents *t*-values. The two significant clusters were collapsed in this figure for the clarity of representation since a common pattern of time distribution and ITC values was evident. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

disappeared and higher-fit showed the same suppression in lower beta compared to lower-fit group, while no remarkable spectral perturbation was observed in the upper beta band in any of the groups.

Previous evidence has shown that event-related desynchronization or power suppression within the alpha and beta band is associated with cortical activation to meet tasks demands rather than reflect the actual performance of the system during the task, while event-related synchronization is associated with deactivated or inhibited cortical networks [10,37]. This is of special relevance given the similar stimulus-related response in EEG power within lower-beta and alpha band in our data, although no statistical differences were reached in the latter. In addition, a positive relationship between reductions in beta suppression and decreased cognitive effort to meet task goals have been proposed by previous studies [10,38]. Thus, interpreted within this framework, one could argue that the reduced lower beta suppression shown by higher-fit to the target stimulus during the first half of the task, represent a fitness-related efficient oscillatory mode of the brain to meet sensorimotor task demands.

The results of upper beta band showed a power increase during the first half of the task in higher-fit participants, although no clear power increase or suppression was shown in the second part of the task in this group or for any temporal block in the case of lower-fit individuals. It is important to note the possibility that the frequency range between 20-40 Hz could comprise mixed activity related to the beta suppression reported above (14-30 Hz) as well as localized gamma oscillations (> 30 Hz). Following this argument and according to previous evidence [39,40], the power increase observed in this frequency band during the first half of the task in higher-fit, may be reflecting a gamma power modulation by the phase of low-frequency oscillations (<14 Hz). Indeed, gamma band is strongly modulated by the phase of low-frequency oscillations and a cross-frequency coupling between low-frequency modulation (mainly theta) and gamma band has been shown to promote sustained attentional control [11].

Overall, taking the evidence described above, our results could therefore represent a better attentional regulation during stimulus processing in higher-fit compared to their lower-fit peers during the first half of the task. Specifically, the neural oscillation pattern of higher-fit points to more efficient neural networks involved in allocation of attention from the target onset, which could be facilitating the integration of visual information with required motor response, finally leading to a greater visuomotor gain related to alertness during the first half of the task. This would support the only previous evidence to date using measures of brain function to determine the mechanisms underlying fitness-related improvements in sustained attention, which indicated that higher-fit participants were better at activating and adapting neural processes involved in cognitive control to meet and maintain task goals [4,41]. In addition, since sustained attention can be understood as an executive function [42], our results are compatible with a model in which theta long-range coupling indicates integration of sensory information into executive control components of motor behaviour [33].

The differential oscillatory pattern as a function of fitness reported here was limited to the first half of the task. Maintaining a high attentional state is effortful and it is taxed by time-on-task [43], which has been evidenced in our study by the vigilance decrement over time in both groups. Therefore, the disappearance of the differential oscillatory pattern as a function of fitness in the second half of the task might be assigned to a drain of executive control capacities in higher-fit individuals.

The cluster-based approach allowed us to describe the spatiotemporal distribution of the neural oscillation patterns as a function of aerobic fitness without biased previous assumptions. So far, there is limited research on the individual differences in brain function and cognition as a function of fitness by using a neural oscillatory approach. To the best of our knowledge, an approach based on strong a priori spatial and/or spectral limitations is usually employed [44,45] which could be leading to the omission of important information. Therefore, this research field would benefit from this data-driven approach to better describe the general pattern of brain oscillations in different cognitive processes as a function of fitness.

While the current study revealed group differences on stimulus-related spectral perturbations that fit well and could potentially explain the fitness-related improvements in sustained attention, these results should be interpreted with special caution. Given the descriptive nature of the present study and the absence of previous hypotheses regarding fitness in this specific context, it would be bold to make strong statements beyond mere speculation. Indeed, various factors have been described as potential mediators between the regular practice of exercise and the observed brain and cognitive changes [46]. Whatever the final explanation, our study represents therefore a first step towards a better understanding of the brain dynamics underlying the relationship between fitness and cognition in general, and sustained attention in particular.

Data availability statement

All data files are available from the Open Science Framework (OSF): https://osf.io/7gu4y/files/

Declaration of Competing Interest

No conflicting financial, consultant, institutional, or other interests exist.

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