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Oscillatory brain activity during acute exercise: Tonic and transient neural response to an oddball task

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Abstract

Intense physical exercise exerts measurable changes at various physiological levels that are well documented in the literature. However, despite the key role of the brain in processing inputs from internal organ systems and the external environment to coordinate and optimize behavior, little is known about brain dynamics during exercise. The present study investigates tonic and transient oscillatory brain activity in a group of participants performing an oddball task during a single bout of aerobic exercise. Twenty young males (19–32 years) were recruited for two experimental sessions on separate days. EEG activity was recorded during a session of cycling at 80% (moderate-to-high intensity) of VO_{2max} (maximum rate of oxygen consumption) while participants responded to infrequent targets (red square and big blue circle) presented among frequent nontargets (small blue circle). This was compared to a (baseline) light intensity session (30% VO_{2max}) to control any potential effect of dual tasking (i.e., pedaling and performing the oddball task). A cluster-based nonparametric permutations test revealed an increase in power across the entire frequency spectrum during the moderate-to-high intensity exercise compared to light intensity. Furthermore, the more salient target (red square) elicited a lower increase in (stimulus-evoked) theta power in the 80% VO_{2max} than in the light intensity condition. Alpha and lower beta power decreased less in the standard trials (small blue circle) during the moderate-to-high exercise condition than in the light exercise condition. The present study unveils, for the first time, a complex brain activity pattern during vigorous exercise while attending to task-relevant stimuli.

KEYWORDS
brain function, brain rhythms, cluster analysis, EEG, exercise intensity, fitness, oddball

1 | INTRODUCTION

The brain plays a major role during strenuous physical exercise (e.g., cycling or running), managing afferent and efferent information from organs and body systems (Kayser, 2003) as well as monitoring external stimuli that may be potentially relevant for behavior (e.g., bumps, obstacles, cracks, etc.), making physical exercise a highly demanding cognitive task (Walsh, 2014). However, while the dynamics and regulatory mechanisms of body systems and organs like muscles, joints, heart, lungs, etc., under physical exercise are well documented (Ashkenazy, Hausdorff, Ivanov, & Stanley, 2002; Baillet et al., 2017; Ivanov, Hu, Hilton, Shea, & Stanley, 2007; Karasik et al., 2002; McArdle, Katch, & Katch, 2010), little is known about brain dynamics when exercising (Johansen-Berg & Duzel, 2016; Walsh, 2014). Here, we provide novel evidence on oscillatory brain activity during a single 20-min bout of moderate-to-high aerobic exercise to pinpoint brain function under physical exertion while, at the same time, attending to relevant external stimuli presented by means of an oddball task.

Previous studies on brain oscillations during intense physical exercise have mainly reported an activity increase in the alpha frequency band at frontal locations (Boutcher, 1993; Kubitz & Pothakos, 1997; Petruzzello, Landers, Hatfield, Kubitz, & Salazar, 1991). This selective effect of acute exercise on the alpha frequency band in anterior sites has been taken as a potential neural mechanism underlying the beneficial effects of acute exercise on mood (Boutcher, 1993; Lattari et al., 2014; Petruzzello et al., 1991) and cognitive function (Chang, Chu, Wang, Song, & Wei, 2015; Dietrich, 2006). Notably, Crabbe and Dishman (2004), in the only meta-analysis to date addressing this issue, carried out a quantitative synthesis of the results from published studies that examined the effect of acute exercise on brain electrocortical activity. They found that the few studies that explored changes during or after exercise showed increases in all frequency bands that were similar in size to the increase in alpha (Crabbe & Dishman, 2004). Further, these changes did not vary significantly between electrode sites. This meta-analysis failed to report the selective enhancement of frontal alpha during exercise supported by previous empirical research, instead suggesting a power increase across the entire frequency spectrum over the whole brain surface. In fact, Crabbe and Dishman recommended the reporting, if possible, of a broad spectrum of frequencies prior to interpreting changes in brain function in response to exercise. In this line, a recent study from our laboratory (Ciria, Perakakis, Luque-Casado, & Sanabria, 2018) tested empirically this hypothesis, reporting that oscillatory brain activity increased during exercise compared to a resting state and that this increase was higher during moderate-to-high intensity exercise compared to a light intensity exercise baseline condition. The results showed that the global pattern of increased oscillatory brain activity was not specific to any concrete surface localization in slow frequencies, while in faster frequencies this effect was located in parieto-occipital sites. This previous work was focused on the averaged steady-state spectral activation under physical exertion but did not investigate transient modulations of brain rhythms in response to task-relevant stimuli during strenuous physical exercise.

Understanding brain function during intense exercise, as noted above, also requires the study of how relevant external stimuli are processed. Physical exertion like running or cycling involves the monitoring and regulation of internal body systems, as well as focused attention, to process and respond efficiently to the potentially relevant information from the dynamic and highly uncertain external environment (e.g., avoiding a pothole on the road while cycling). Indeed, focused or sustained attention is crucial for proper cognitive function that allows both adaptation to environmental demands and the capacity to modify behavior (Sarter, Givens, & Bruno, 2001). Sustained attention under physical exertion has been traditionally measured by means of oddball tasks whereby participants had to detect infrequent and unexpected targets presented among frequent nontarget stimuli (Grego et al., 2004; Gwin, Gramann, Makeig, & Ferris, 2010; Schmidt-Kassow, Heinemann, Abel, & Kaiser, 2013; Yagi, Coburn, Estes, & Arruda, 1999). This unspeeded task is particularly suitable for research on brain function during physical exercise as it has low motor demands and involves high uncertainty of the target onset. In fact, together with temporal uncertainty, the low probability of target appearance has been shown to be one of the major factors in taxing sustained attention (Parasuraman & Mouloua, 1987).

To date, behavioral studies have pointed to an enhanced attentional processing while participants exercise at moderate-to-high intensity (Chang, Labban, Gapin, & Etnier, 2012; Verburgh, Konigs, Scherder, & Oosterlaan, 2014) while lower or higher intensities (as a function of the participant's anaerobic threshold) result in performance decline or in no significant variations (with respect to peak performance; e.g., Chmura, Krysztofiak, Ziemba, Nazar, & Kaciuba-Uścilko, 1997; González-Fernández, Etnier, Zabala, & Sanabria, 2017). In addition to behavioral measurements, several studies have provided insights into how neural correlates of (task-relevant) stimulus processing are modulated during moderate-to-high intensity exercise by means of ERPs (Bullock, Cecotti, & Giesbrecht, 2015; Grego et al., 2004; Gwin et al., 2010; Schmidt-Kassow et al., 2013; Yagi et al., 1999). Here, we take a step further by analyzing, for the first time, power spectral changes time-locked to the (task) stimulus as a way of depicting brain oscillations associated with the processing of relevant stimuli under intense physical exercise.

Event-related spectral perturbations (ERSPs) relate to transient decrease or increase in oscillatory brain activity locked to an event, which is thought to reflect the state of synchrony in a population of neurons (Pfurtscheller, 1992; Pfurtscheller & Aranibar, 1977), and may provide complementary information to that of the ERPs. Even though the analysis of ERSP could further elucidate the underlying mechanism of attentional processing under physical exertion, no study so far has explored neural responses during a single bout of exercise using this approach. This is particularly noteworthy since brain oscillatory activity has been shown to be a key mechanism supporting sustained attention performance (Klimesch, Sauseng, Hanslmayr, Gruber, & Freunberger, 2007).

To achieve the objectives of this study, our participants performed a three-stimulus oddball task characterized by a target/nontarget difficulty discrimination and the presence of a very salient target stimulus that would lead to a high stimulus-locked neural response. Notice that several authors have suggested that the conflicting findings of previous ERPs studies may be due to the use of oddball tasks that were not challenging enough to yield significant effects under physical exertion (Clayton, Yeung, & Cohen Kadosh, 2015; Hillman, Pontifex, & Themanson, 2009). For instance, Yagi and collaborators (1999) found that participants under physical exertion exhibited a smaller P300 amplitude and shorter P300 latency than in pre-exercise measures. However, Grego et al. (2004) found a steady increase of P300 amplitude and latency during exercise. By implementing a challenging oddball task (i.e., increasing the difficulty of target/nontarget discrimination), we aimed to amplify the possible behavioral and neural differences as a function of exercise intensity. Crucially, participants completed the oddball task while exercising at two different intensities (in two separate experimental sessions), corresponding to the 80% and 30% of their VO_{2max} (i.e., maximum rate of oxygen consumption). This selection was motivated by previous evidence pointing to moderate-to-high acute exercise (between 60% and 80% VO_{2max}) as the key intensity to induce cognitive enhancement (Brisswalter, Collardeau, & René, 2002; Chang & Etnier, 2009; Hillman, Kamijo, & Pontifex, 2012). The 30% condition was included as the light intensity exercise baseline (instead of a rest nonexercise condition) to control, as much as possible, potential dual-tasking effects (i.e., participants were both exercising and performing the oddball task).

We expected, based on previous evidence (Crabbe & Dishman, 2004; Ciria et al., 2018), a higher power increase across the entire frequency spectrum during moderate-to-high intensity exercise in comparison with the (baseline) light intensity exercise. This finding would once again jeopardize the extended idea of a selective effect in the alpha band (Ciria et al., 2018). Behaviorally, we predicted higher cognitive performance in the moderate-to-high exercise condition than in the light intensity exercise condition. We also expected a distinctive oscillatory brain ERSP pattern during moderate-to-high exercise (compared to the light intensity exercise), although we did not have clear hypotheses about the direction and nature of the effects. For this reason, we implemented a stepwise cluster-based, nonparametric permutations test without prior assumptions on any frequency range or site of interest (see Method for details).

2 | METHOD

2.1 | Participants

We recruited 20 young males with a high level of aerobic fitness (age between 18–31 years old, average age 23.9 years) from the University of Granada (Spain). All participants met the inclusion criteria of reporting at least 8 hr of cycling or triathlon training per week, normal or corrected-to-normal vision, reported no neurological, cardiovascular, or musculoskeletal disorders, and were taking no medication. Note that high-fit cyclists and triathletes were selected because they are capable of maintaining a pedaling cadence at moderate-to-high intensity during long periods of time. Furthermore, they are able to keep a fixed posture over time, which reduces EEG movement artifacts considerably. Their fitness level was verified by an incremental effort test (see below). Participants were required to maintain a regular sleep-wake cycle for at least 1 day before each experimental session and to abstain from stimulating beverages or any intense physical activity 24 hr before each session. All subjects gave written informed consent before the study. The protocol was in accordance with both the ethical guidelines of the University of Granada and the Declaration of Helsinki.

2.2 | Apparatus and materials

All participants were fitted with a Polar RS800 CX monitor (Polar Electro Öy, Kempele, Finland) to record their heart rate 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 analyzer (CareFusion GmbH, Germany) to provide a measure of gas exchange during the effort test. Oddball stimuli were presented on a 21" BENQ screen maintaining a fixed distance of 100 cm between the head of participants and the center of the screen. E-Prime software (Psychology Software Tools, Pittsburgh, PA) was used for stimulus presentation and behavioral data collection.

2.3 | Fitness assessments

Participants came to the laboratory at least 1 week before the first experimental session to provide the informed consent, complete an anthropometric evaluation (height, weight, and body mass index), and to familiarize with the oddball task. Subsequently, they performed an incremental cycle-ergometer test to obtain their VO_{2max}, which was used in the following experimental sessions to adjust the exercise intensity individually. The incremental effort test started with a 3-min warm-up at 30 watts (W), with the power output increasing 10 W every minute. Each participant set his preferred cadence (between 60–90 revolutions per min^{-1}) during the warm-up period and was asked to maintain this cadence during the entire protocol. The test began at 60 W and was followed by an incremental protocol of 30 W every 3 min. Each step of the incremental protocol consisted of 2 min of stabilized load and 1 min of progressive load increase (5 W every 10 s). The oxygen uptake (VO_2 ml • min^{-1} • kg^{-1}), respiratory exchange ratio (i.e., CO_2 production • O_2 consumption^{-1}), relative power output (W • kg^{-1}) and heart rate (bpm) were continuously recorded throughout the test.

2.4 | Experimental sessions

Participants completed two counterbalanced experimental sessions of approximately 100 min each. To avoid possible fatigue and/or training effects, visits to the laboratory were scheduled on different days allowing 48–72 hr between sessions. On each experimental session, after a 10-min warm-up on a cycle-ergometer at a power load of 30% of their individual VO_{2max}, participants performed an oddball task for 20 min while pedaling either at 30% (light intensity exercise session) or 80% (moderate intensity exercise session) of their VO_{2max}. Upon completion of the oddball task, a 10-min cool-down period at 30% of intensity followed (see Table 1). Each participant set his preferred cadence (between 60–90 revolutions per min^{-1}) before the warm-up and was asked to maintain this cadence throughout the session in order to match conditions, as much as possible, in terms of dual-task demands.

2.5 | Oddball task

The visual oddball task was based on that reported in Sawaki and Katayama (2007). It consisted of a random presentation of three visual stimuli: a frequent small blue circle (approximately 1.15º × 1.15º), a rare big blue circle (approximately 1.30º × 1.30º), and a rare red square (approximately 2.00º × 2.00º). Small blue circles were considered as standard stimuli (nontarget), while big blue circles (Target 1) and red squares (Target 2) were considered as target stimuli. Stimuli were displayed sequentially on the center of the screen on a black background. Each trial started with the presentation of a blank screen for 1,200 ms. Then, the stimulus was presented at a random time interval (between 0 and 800 ms) for 150 ms. Participants were instructed to respond to both targets by pressing a button connected to the cycle-ergometer handlebar with the thumb of their dominant hand and to not respond when standard stimuli were shown. Participants were encouraged to respond as accurately as possible. The target stimuli were randomly presented in 20% of trials (10% of Target 1, 10% of Target 2) and the nontarget stimulus in the remaining 80% of trials. A total of 600 stimuli were presented. The task lasted for approximately 20 min. No breaks were allowed.

TABLE 1 Mean and 95% confidence intervals of descriptive exercise-intensity parameters for the moderate-to-high intensity and light intensity conditions

	Moderate-to-high intensity (80% VO_{2max})	Light intensity (30% VO_{2max})
Exercise period parameters		
Mean power load (W)	233.4 [222, 242]	87.5 [83, 90]
Mean relative power load (W/kg)	3.0 [2.8, 3.2]	1.1 [1.0, 1.2]

Note. W = watts; kg = kilograms.

2.6 | EEG recording and analysis

EEG data were recorded at 1000 Hz using a 30-channel actiCHamp System (Brain Products GmbH, Munich, Germany) with active electrodes positioned according to the 10–20 EEG International system and referenced to the Cz electrode. The cap was adapted to individual head size, and each electrode was filled with Signa Electro-Gel (Parker Laboratories, Fairfield, NJ) to optimize signal transduction. Participants were instructed to avoid postural movements as much as possible and to keep their gaze on the center of the screen during the task. Electrode impedances were kept below 10 kΩ. EEG preprocessing was conducted using custom MATLAB scripts and the EEGLAB (Delorme & Makeig, 2004) and Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen, 2011) MATLAB toolboxes. EEG data were resampled at 500 Hz, band-pass filtered offline from 1 and 40 Hz to remove signal drifts and line noise, and rereferenced to a common average reference. Horizontal electrooculograms (EOG) were recorded by bipolar external electrodes for the offline detection of ocular artifacts. The potential influence of electromyographic (EMG) activity in the EEG signal was minimized by using the available EEGLAB routines (Delorme & Makeig, 2004). Independent component analysis was used to detect and remove EEG components reflecting eyeblinks (Hoffmann & Falkenstein, 2008). Abnormal spectra epochs that spectral power deviated from the mean by ±50 dB in the 0–2 Hz frequency window (useful for catching eye movements) and by +25 or −100 dB in the 20–40 Hz frequency window (useful for detecting muscle activity) were rejected. On average, 2.54% of trials per participant were discarded.

The present experiment was carefully designed following all methodological and data processing recommendations to obtain reliable EEG data under physical exertion (see Pontifex & Hillman, 2008; Thompson, Steffert, Ros, Leach, & Gruzelier, 2008). The signal-to-noise ratio was maximized by (a) choosing stationary cycling with fixed pedaling cadence to minimize movement-related artifacts, (b) testing a sample of well-trained cyclists accustomed to maintain a fixed posture over prolonged periods of time, (c) using active electrodes and a cap fixation system that reduces electrode impedance), (d) using artifact and noise reduction techniques (band-pass filter and rejection of single trials based on spectral power deviation in concrete frequency ranges), and (e) including a control light intensity exercise condition (instead of a nonexercise condition) matched, as much as possible, in terms of movement demands.

2.6.1 | Spectral power analysis

Electrodes presenting abnormal power spectrum were identified via visual inspection and replaced by spherical interpolation. Processed EEG data from each experimental period (warm-up, exercise, cool down) were subsequently segmented to 1-s epochs. The spectral decomposition of each epoch was computed using fast Fourier transform (FFT) applying a symmetric Hamming window, and the obtained power values were averaged across experimental periods.

2.6.2 | ERSP analysis

Task-evoked spectral EEG activity was assessed by computing ERSP in epochs extending from –500 ms to 500 ms time-locked to stimulus onset for frequencies between 4 and 40 Hz. Spectral decomposition was performed using sinusoidal wavelets with three cycles at the lowest frequency and increasing by a factor of 0.8 with increasing frequency. Power values were normalized with respect to a − 300 ms to 0 ms prestimulus baseline and transformed into the decibel scale.

2.7 | Statistical analysis

Spectral power main effects of intensity condition (light intensity, moderate-to-high intensity) were separately tested for significance at each period (warm-up, exercise, cool down). We used a stepwise, cluster-based, nonparametric permutations test (Maris & Oostenveld, 2007; Fieldtrip toolbox) without prior assumptions on any frequency range or area of interest. The algorithm performed a *t* test for dependent samples on all individual Electrodes × Frequencies Pairs and clustered samples with positive and negative *t* values that exceeded a threshold ($p < 0.05$, two-tailed) based on spatial and spectral adjacency. These comparisons were performed for each frequency bin of 1 Hz and for each electrode. Cluster-level statistics were then calculated by taking the sum of the *t* values within each cluster. The trials from the two data sets (light intensity, moderate-to-high intensity) were randomly shuffled, and the maximum cluster-level statistic for these new shuffled data sets was calculated. The above procedure was repeated 5,000 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.

In addition, ERSP main effects of intensity condition (light intensity, moderate-to-high intensity) for each stimulus (Target 1, Target 2, and standard) were also analyzed by applying the cluster-based permutations test. In order to reduce the possibility that the Type II error rate was inflated by multiple comparisons correction, we grouped data into four frequency bands: theta (4–8 Hz), alpha (8–14 Hz), lower beta (14–20 Hz), and upper beta 1 (20–40 Hz). Note that the time window of interest in target trials was restricted to the first 300 ms after target onset in order to avoid an overlap with behavioral responses based on average reaction time (RT). The time window of interest for standard trials was fixed to the first 500 ms after the stimulus onset.

Behavioral data from both sessions were analyzed using a within-participant factor of intensity condition (light intensity, moderate-to-high intensity) for RT and accuracy (ACC) as dependent variables. All analyses were completed using statistical nonparametric permutation tests with a Monte Carlo approach (Ernst, 2004; Pesarin & Salmaso, 2010).

The EEG and behavioral data are available at the ZENODO repository: https://zenodo.org/record/1404656#.W4ZeM5P-jOQ.

3 | RESULTS

3.1 | Behavioral performance

Table 1 provides mean and 95% confidence intervals of descriptive exercise-intensity parameters.

The analysis of participants' RTs and ACC (see Figure 1) did not reveal statistically significant differences between intensity conditions (all *p*s > 0.05).

3.2 | Spectral power analysis

The analysis of tonic spectral power showed a significant difference between intensity conditions for the exercise period (all *p*s < 0.025). The cluster-based permutation tests revealed differences between intensity conditions in low frequencies (1–5 Hz), cluster $p < 0.001$ (28 electrodes), and also in fast frequencies (8–40 Hz), cluster $p = 0.02$ (18 electrodes). The analysis showed an overall increase in the power of frequencies during the moderate-to-high intensity exercise period in comparison to light intensity (see Figure 2). There were no statistically significant between-conditions differences in warm-up and cool down periods (all cluster *p*s ≥ .1).

3.3 | ERSP analysis

Figure 3 shows the time-locked oscillatory activity of the oddball task during both exercise periods. The analysis of the ERSP revealed a significant difference between intensity

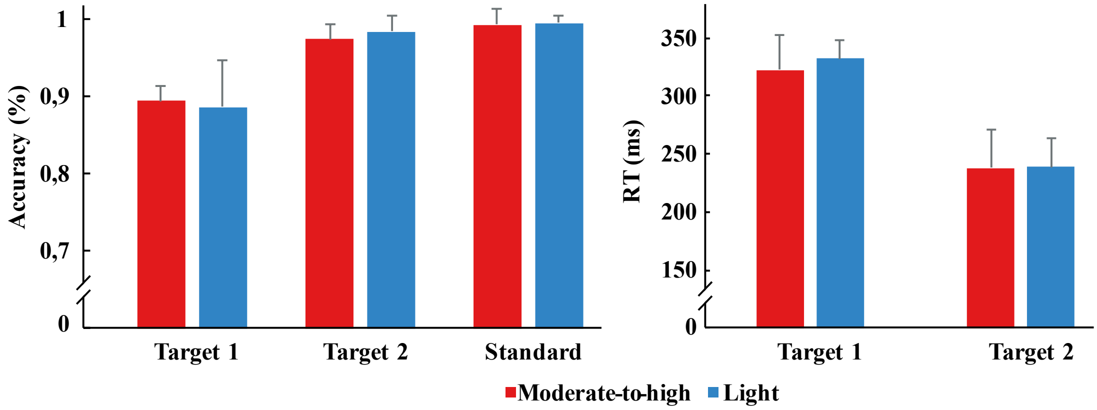

FIGURE 1 Mean and 95% confidence intervals of behavioral performance (accuracy and reaction time) for the moderate-to-high intensity (red) and light intensity conditions (blue). The analysis of accuracy and RT for standard, Target 1, and Target 2 stimuli did not yield significant differences

conditions for standard trials in alpha and lower beta bands and for the Target 2 trials in theta band (all *p*s < 0.025). The cluster-based permutation tests revealed differences between intensity conditions in the alpha band (8–14 Hz) in the latency range from 400 to 500 ms poststimulus, cluster $p < 0.013$ (16 electrodes), showing a higher alpha spectral power (or lower power suppression) during moderate-to-high intensity exercise compared to light intensity (see Figure 4a). The analysis also revealed differences between intensity conditions in the lower beta band (14–20 Hz) in the latency range from 450 to 500 ms poststimulus, cluster $p < 0.017$ (8 electrodes), showing a higher spectral power (or lower power suppression) in the moderate-to-high intensity condition than in the light intensity condition (see Figure 4b).

The analysis of Target 2 trials showed significant differences between intensity conditions in theta band (4–8 Hz) in the latency range from 230 to 270 ms poststimulus, cluster $p < 0.008$ (seven electrodes). Target 2 trials (red squares) during moderate-to-high intensity exercise condition evoked lesser theta power than during light intensity exercise condition (see Figure 4c). The analysis of the other frequency bands for Target 1, Target 2, and standard trials did not yield significant differences (all *p*s ≥ 0.05).

4 | DISCUSSION

The present study investigated oscillatory brain activity during a single bout of aerobic exercise (cycling) at 80% of the maximum aerobic capacity compared to a light intensity exercise (control) session, while participants performed a visual oddball task. We found that acute exercise at moderate-to-high intensity induced a complex brain activity pattern at the tonic and transient (event-related) level, which was characterized by a higher spectral power across the entire EEG frequency spectrum, with the exception of the theta frequency range, compared to light intensity exercise. Interestingly, the heightened spectral power activity during moderate-to-high intensity exercise was accompanied by a lesser power suppression of alpha and lower beta bands time-locked to the standard stimuli and a lesser power increase of the theta band to the more salient target, compared to the light intensity exercise.

The overall power increase across the frequency spectrum during moderate-to-high intensity exercise compared to light intensity is in line with previous research (Ciria et al., 2018; Crabbe & Dishman, 2004). Indeed, the only meta-analysis to date that has addressed this issue (Crabbe & Dishman, 2004) found no evidence of the selective effect of exercise on the alpha frequency band at frontal locations suggested by previous empirical research (Boutcher, 1993; Kubitz & Pothakos, 1997; Petruzzello, Hall, & Ekkekakis, 2001; Petruzzello et al., 1991). Here, the between-intensity differences were not specific to brain location in slow frequencies, while in faster frequencies the differences arose from parieto-occipital sites. These results partially contradict previous studies that have shown changes in oscillatory brain activity during exercise localized in anterior sites (Bailey, Hall, Folger, & Miller, 2008; Kubitz & Pothakos, 1997).

Several studies have suggested that the theta frequency band is selectively enhanced by the presentation of novel stimuli, linking it to the orienting responses associated with novelty processing (Demiralp, Ademoglu, Comerchero, & Polich, 2001; Demiralp, Ademoglu, Istefanopulos, Başar-Eroglu, & Başar, 2001). Moreover, alpha activity suppression has been associated with cognitive engagement to the task (Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007) during oddball paradigms (Yordanova & Kolev, 1998; Yordanova, Kolev, & Polich, 2001). Thus, the present theta and alpha results could well reveal an enhanced ability to attend to relevant external stimuli during moderate-to-high intensity exercise that was not captured by

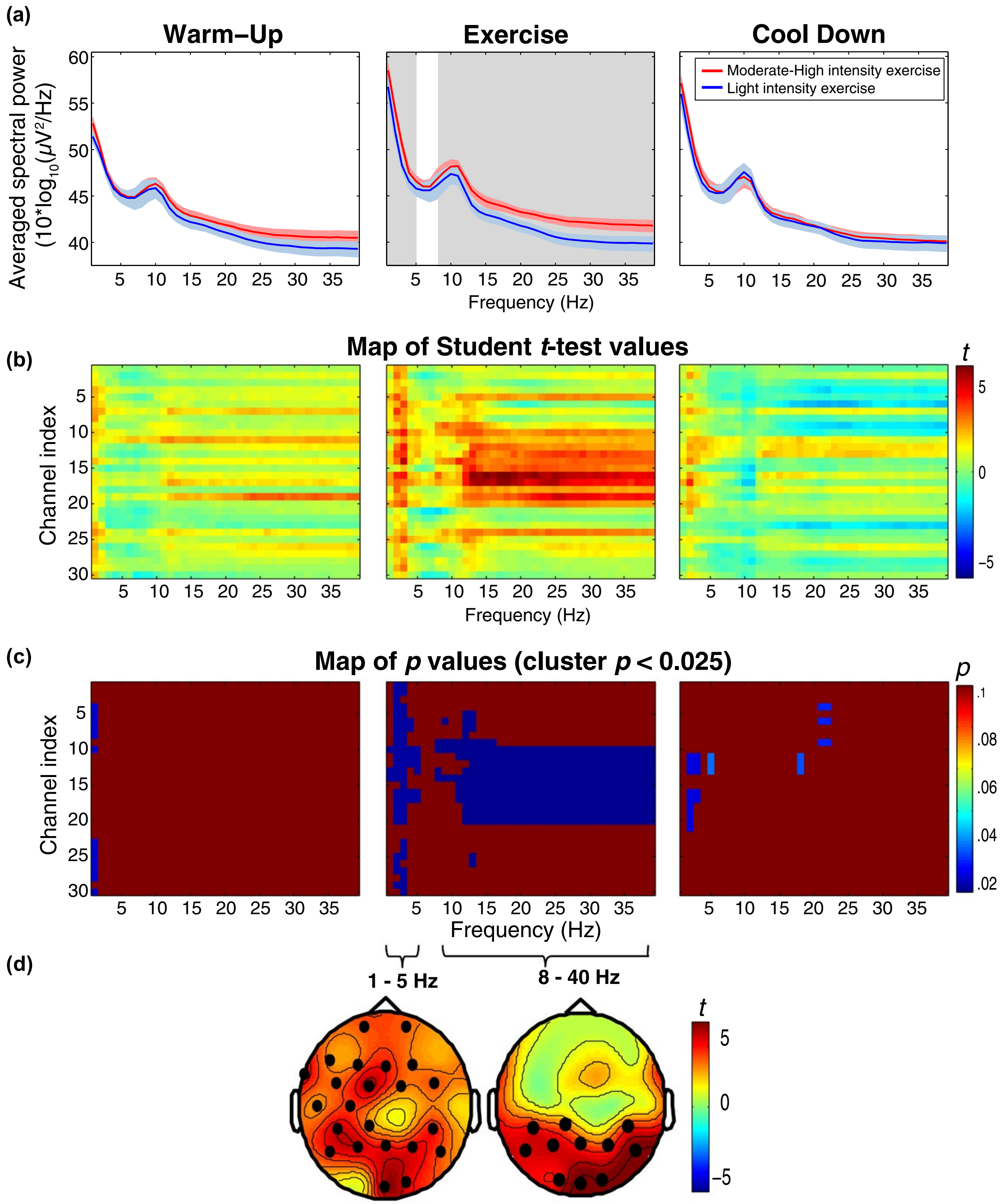

FIGURE 2 Modulation of brain power spectrum as a function of exercise intensity. (a) Differences in the averaged EEG power spectrum across subjects between moderate-to-high intensity (red) and light intensity (blue) exercise at the three experimental periods. Red and blue shaded areas represent 95% confidence intervals. Statistically significant differences are marked by gray area. During exercise, the overall power of the entire frequency spectrum, with exception of the theta range, was higher during moderate-to-high intensity exercise compared to light intensity exercise. (b) Parametric paired *t*-test maps comparing the relative power across frequency bands (*x* axes) and channels (*y* axes) during moderate-to-high intensity and light intensity exercise (blue: decreases; red: increases). (c) Each image illustrates the statistical significance (*p* values) of the *t* maps depicting only the significant clusters with $p < 0.025$. (d) Topographies depict *t*-test distribution in all electrodes, showing the spatial characteristics of the increase in power of low frequencies across the whole surface localization during moderate-to-high exercise and the increase in high frequencies in parieto-occipital areas during moderate-to-high exercise. No significant between-intensity differences were found at warm-up and cool down

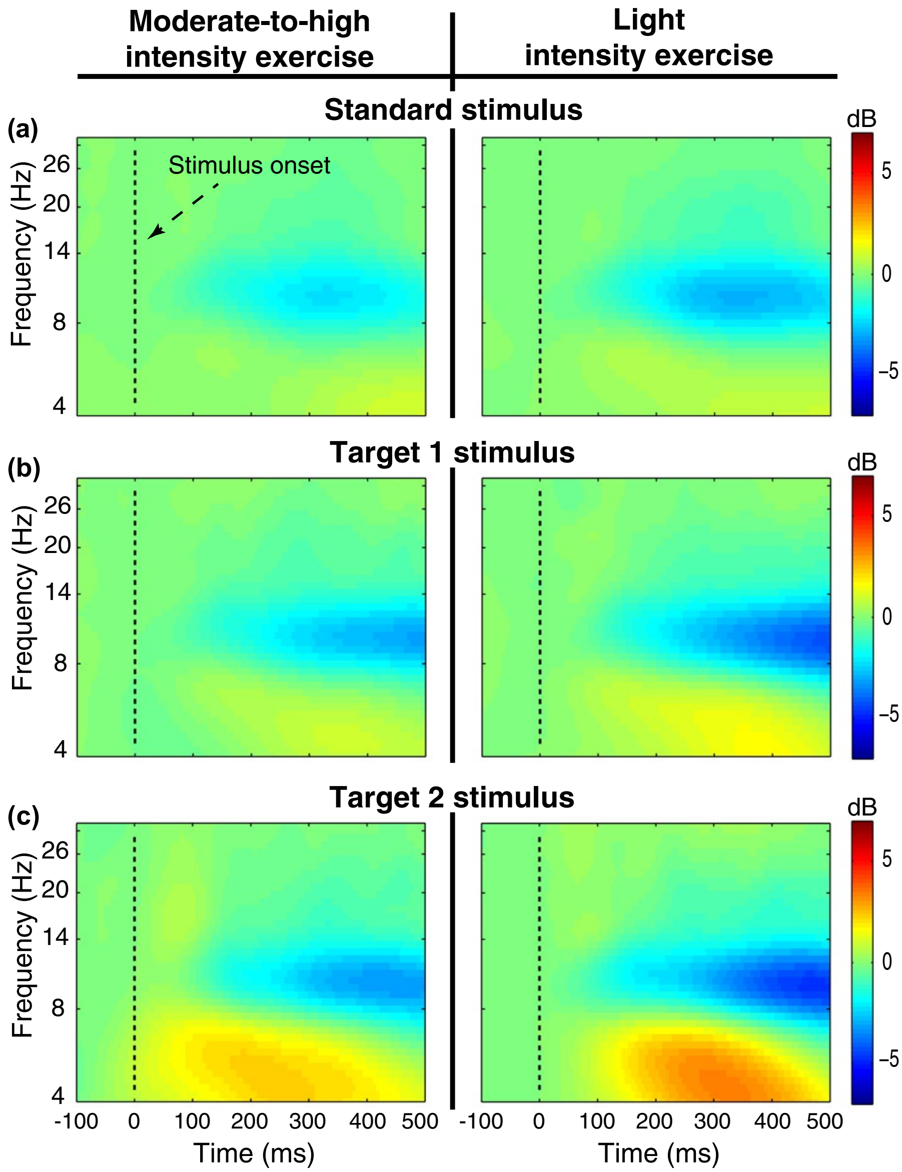

FIGURE 3 Event-related spectral perturbation of oddball task during exercise. Time-locked spectral power averaged across all channels during moderate-to-high intensity (left) and light intensity (right) exercise for all stimuli (standard, Target 1, Target 2). Each panel illustrates time-frequency power across time (*x* axes) and frequency (*y* axes) during moderate intensity and light intensity exercise (blue: decreases; red: increases)

the behavioral index of performance (e.g., due to a ceiling effect). On the contrary, they could simply reflect neural changes that were not related to sustained attention and/or acute exercise. Even if our study was designed to tax sustained attention, the lack of behavioral differences makes any interpretation highly speculative. In any case, the reduced theta power to Target 2 trials (the more salient stimuli) and the lower suppression of alpha to the standard trials, together with the lower beta power during the moderate-to-high intensity exercise session when compared to the light intensity session, suggest that the effect of acute exercise over stimulus processing cannot be explained as a mere overall increase of oscillatory brain activity.

Electrocortical activity under physical exertion is often contaminated by artifacts of noncerebral origin (breathing, heart rate, sweating, increased movement, etc.). Higher intensity exercise could therefore result in a lower signal-to-noise ratio. However, the present experiment was carefully designed following all methodological and data processing recommendations to obtain reliable EEG data under physical exertion (see Pontifex & Hillman, 2008; Thompson et al., 2008). These practical aspects of EEG recording, along with the increasingly sophisticated recording systems, have demonstrated the offer of a promising means for minimizing, if perhaps not entirely eradicating, the issues with movement-related EEG artifacts (e.g., Brümmer, Schneider, Strüder, & Askew, 2011;

Ciria et al., 2018; Holgado et al., 2018; Ludyga, Gronwald, & Hottenrott, 2016; Schmidt-Kassow et al., 2013; Schneider, Brümmer, Abel, Askew, & Strüder, 2009). In addition, the choice of a light intensity exercise condition as a control condition (instead of a nonexercise condition) offers a proper means of matching, as much as possible, both conditions in terms of motion-related artifacts, but also in terms of dual-task demands. If we assume that movement coordination is a cognitive task in itself with its own load and specific requirements for attentional resources allocation (e.g., Walsh, 2014), a different exercise intensity would imply a different cognitive load. However, a control condition involving quite

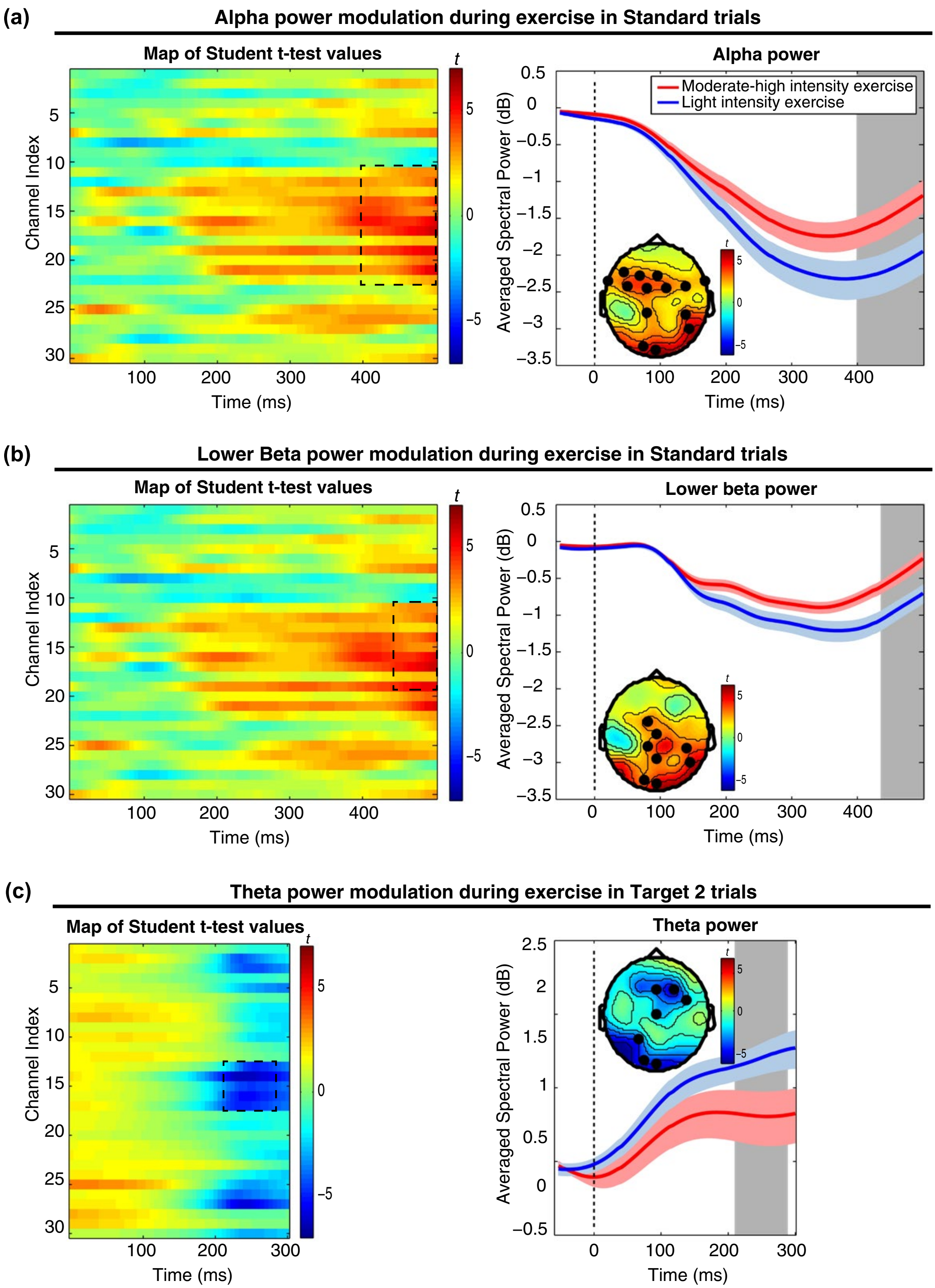

FIGURE 4 Event-related spectral perturbation significant main differences as a function of intensity condition. (a) Alpha frequency band parametric paired *t*-test maps comparing the averaged spectral power across subjects over time (*x* axes) and frequency (*y* axes) during moderate-to-high intensity and light intensity exercise in standard trials. The enclosed areas denote significant cluster of channels and time with $p < 0.025$. Right panel shows alpha power across time at the occipital-parietal cluster in standard trials. Shaded area represents the latency range where significant differences between intensity conditions were found. Red and blue shaded areas represent 95% confidence intervals. The topography depicts the *t*-test distribution across surface localizations, showing the spatial characteristics of the lower power suppression of alpha during moderate-to-high exercise compared to light intensity exercise condition. (b) Parametric paired *t*-test maps comparison between moderate-to-high exercise and light exercise in lower beta frequency band to standard trials. Right panel shows the lower power suppression of beta during moderate-to-high exercise compared to the light intensity exercise condition across time at the parieto-occipital cluster in standard trials. (c) Theta frequency band parametric paired *t*-test maps comparing moderate-to-high intensity and light intensity exercise in Target 2 trials. Right panel shows theta power across time at the globally localized cluster in Target 2 trials, revealing the spatial characteristics of the lower power increase of theta during moderate-to-high exercise compared to the light intensity exercise condition. The time window of interest in target trials was restricted to the first 300 ms in order to avoid neural activity overlapping with behavioral responses

similar coordination demands (in our case, pedaling at low intensity) is essential to interpreting posterior cognitive benefits as induced by physical exertion alone, minimizing the possible confound of prior engagement in motor coordination. Interestingly, although the moderate-to-high intensity exercise could imply higher demands, the ERSP results showed a lower event-related brain oscillatory activity in comparison to the light intensity exercise. Therefore, we believe that any variation in brain function was due to the physiological changes induced by the particular exercise intensity.

Exercising elicits a wide set of physiological changes such as increases in core temperature, cortical blood flow, heart rate, and catecholamine concentration (McMorris & Hale, 2015), which have generally been recognized as a potential mechanism underlying the effect of acute exercise on brain function. Interestingly, we found a higher global increase of oscillatory brain activity during the moderate-to-high intensity session than the light intensity session. This latter result is consistent with recent accounts that have linked acute exercise to enhanced activation/arousal (that relates to the overall activation/excitability of cortical neurons; Enders et al., 2016; Langner & Eickhoff, 2013; Oken, Salinsky, & Elsas, 2006). However, the ERSP results in our study suggest that the effect of acute exercise cannot be explained as an overall increase of oscillatory brain activity but to a task-specific brain function during exercise (at moderate-to-high intensity).

To conclude, the present study contributes to the understanding of brain dynamics during acute exercise demanding both the monitoring of internal and external inputs, possibly one of the most challenging behaviors.

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