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Research article

Acute Effects of an Incremental Exercise Test on Psychophysiological Variables and Their Interaction

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Abstract

Besides neurophysiological effects, the potential influence of exercise induced strains in terms of peripheral physiology or subjectively perceived stress as well as their possible reciprocal relation is not clearly understood yet. This study aimed to analyze effects of increasing exercise intensity on brain activity (spontaneous EEG), heart rate variability (HRV) and rating of perceived exertion (RPE) by means of a graded exercise test (GXT). Fifteen participants performed an open-loop GXT on a bicycle ergometer beginning at 50W and an increment of 50W every three minutes. Rest measurements were conducted pre- (5 min) and especially post-exercise (15 min) to analyze (neuro-) physiological prolonged effects. EEG and HRV were measured in parallel before, during (including RPE) and after GXT. Brain activity showed next to already determined effects (e.g. increased (pre)frontal theta, alpha and beta power) a particular activation of the temporal lobe after GXT compared to pre-resting state. HRV frequency parameters significantly decreased following GXT. Recovery process revealed a significant alteration of EEG and HRV towards pre-resting state with prolonged effects in the temporal lobe. Correlation analysis during GXT led to moderately negative effects of EEG total spectrum power and HRV frequency parameters. Frontopolar and temporal lobe revealed noteworthy negative correlated effects with HRV. Referring to RPE, solely temporal gamma activity correlated moderately positive with RPE. Recovery exposed only in the temporal cortex a moderately negative correlation to HF power. Thus, further analysis of the temporal brain lobe in context with exhausting physical exercise comprising induced regulation of cardiovascular stress and perceived exertion is promoted. These results indicate a brain lobe specific relation to peripheral physiology as well as perceived strain with a dependency of rest or exercise condition. Therefore, enough incentives are given to encourage further analysis of a connection between the (neuro-) physiological system as well as subjectively perceived exertion.

Key words: EEG, graded exercise, exhaustive task, RPE, HRV, recovery.

Introduction

After first reductionistic approaches to understand the interactions of physical activity, neuronal control and cognitive performance, an increasing trend towards a more holistic understanding can be observed. A large number of research papers published in recent decades dealing with the influence of physical activity on cognitive performance (Chang et al., 2012; Cox et al., 2016; Crabbe and Dishman, 2004; Etnier et al., 1997) reflects the significance of this topic until today (Etnier and Chang, 2019; Sun et al., 2020). Here, research can be distinguished between effects regarding the actual cognitive performance output, from a psycho-behavioral point of view, and those related to (neuro-) physiological processes that are assumed to be underlying conditions of the observed behavior. While the cognitive performance output of physical activity is widely accepted, psycho-behavioral effects as well as underlying (neuro-) physiological processes and relationships are still not completely understood. Here, mainly studies covering three areas with specific tools for measurement can be differentiated. One area that can be associated with the connection of metabolism and vagal system applies heart rate variability (HRV) measurements. Analyzing HRV during exercise reveals information about the sympatho-vagal balance via the amount of interoceptive stimuli sent from the heart due to autonomic changes (Buchheit et al., 2007). The second area can be ascribed to the central nervous system and its connection to the vagal system measured by means of electroencephalography (EEG) frequency-band specific brain activity. Studies already indicate a connection of different EEG frequency bands to the autonomic nervous system (ANS) regulation (Ako et al., 2003; Ehrhart et al., 2000; Garcia et al., 2011; Kuo et al., 2016; Tang et al., 2009; Triggiani et al., 2016). Referring to neurophysiological analysis, EEG as a simple and mobile method to measure electrical brain activity in context of physical activity is often used (Bertollo et al., 2019; di Fronso et al., 2019; di Fronso et al., 2017; Park et al., 2015). Furthermore, it presents an applicable tool to achieve, e.g. via neuro-feedback, an enhancement of performance (di Fronso et al., 2017). For a brief overview of brain frequency bands and their functionality see (Malik and Amin, 2017). Also the determination of individual alpha peak frequency (iAPF) as a measure of information processing (Klimesch et al., 1996), attention (Mierau et al., 2017) and arousal (Jann et al., 2010; Lambourne and Tomporowski, 2010) is considered to be of interest in the context of performance improvement, e.g. in relation to psycho-behavioral processes. The third area can be assigned to the psychological level measured by means of the rate of perceived exertion (RPE). RPE is one of the main psycho-behavioral output control systems during exercise (St Clair Gibson et al., 2006) and defines an important factor for evaluation of internal load, e.g. for monitoring training (Impellizzeri et al., 2004; 2019).

Despite some commonalities, a major reason for partially contradictory results within these three branches of research can be seen in the type of analyzed movement, e.g. fine (Cuffaro, 2011) or gross motor skills (Esposito and Vivanti, 2013). Due to the higher influence of gravitational

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and inertial forces as well as due to the involvement of large muscle groups, gross motor movements are accompanied by different control mechanisms and by a clearly increased physiological strain, i.e. typically increased heart rate and associated changes in regulation of the ANS as well as in perceived exertion. How these different types of strain are interacting in context of gross motor movements is not completely clarified. We will focus on gross motor movements since they are more adequate to the majority of sports than fine motor movements. Further investigations of psychophysiological processes provoked through gross motor movements could support the elucidation of the interacting brain and cardiovascular system as well as performance outputs on behavioral level, which could be beneficial in the conception of therapy, rehabilitation and individual training.

A graded exercise test (GXT) signifies an applicable method to provoke exercise induced reactions in all three areas mentioned due to the increasing intensity until exhaustion. As the overview of GXT-conducted studies in Table 1 shows, to our knowledge, all these three areas have yet not been analyzed in parallel. Neither before and after nor during a GXT execution, HRV, EEG and RPE parameters were measured simultaneously. This pertains also for the concurrent assessment of only HRV and EEG. Thus, an interaction may only be inferred indirectly from results of previous studies investigating brain (Abeln et al., 2015; Bailey et al., 2008; Brümmer et al., 2011; di Fronso et al., 2019; Dykstra et al., 2019; Edwards et al., 2016; Gutmann et al., 2018; Jung et al., 2015; Mechau et al., 1998; Moraes et al., 2007; Robertson and Marino, 2015; Schneider et al., 2013), HRV (Banach et al., 2004; Candido et al., 2015; Cruz et al., 2017; da Silva et al., 2017; Duarte et al., 2014; Michael et al., 2017; Shiraishi et al., 2018; Yamamoto et al., 1992) and RPE (Duarte et al., 2014; Faulkner and Eston, 2007; Moraes et al., 2007) effects separately. Therefore, research interest rises to simultaneously study the reaction of the (neuro-) physiological system as well as the perceived exertion to a GXT execution.

Regarding the area of physiological effects induced by physical exercise associated to HRV analysis, one GXT study showed after the exercise mostly highly significant reductions of time (SDNN, RMSSD) and all spectral parameters (TP, LF, HF, LF/HF ratio) (Banach et al., 2004). The reduction of SDNN and especially RMSSD indicated a lower activity of the parasympathetic system, which is quite obvious as a consequence of an exhaustive exercise. Another study on HRV (da Silva et al., 2017) identified higher LF and lower HF power during the GXT compared with control condition, i.e. sitting motionless on a bicycle ergometer, portending an increased sympathetic heart rate activity. Referring to the recovery after a GXT, a HRV analysis has not yet been explicitly conducted, to our knowledge. Studies analyzing a steady strenuous physical activity revealed an increase of HRV frequency parameters during 30 minutes recovery towards pre-exercise level (Kaikkonen et al., 2008). But still there was a remaining difference to baseline values up to one hour after exercise (Spring et al., 2018) indicating no complete recovery of the autonomic cardiovascular system. All mentioned HRV studies show an alteration of the ANS during and after exercise.

Table 1. Overview of GXT research with analyzed RPE, HRV or EEG effects.

Study	Pre-GXT		During-GXT			Post-GXT	
	HRV	EEG	RPE	HRV	EEG	HRV	EEG
Yamamoto, Hughson, & Nakamura, 1992				+			
Mechau, Mücke, Weiss, & Liesen, 1998		+			+		+
Banach et al., 2004	+			+			
Faulkner & Eston, 2007			+				
Moraes et al., 2007		+	+				+
Bailey, Hall, Folger, & Miller, 2008		+			+		+
Brümmer, Schneider, Strüder, & Askew, 2011		+			+		+
Schneider, Rouffet, Billaut, & Strüder, 2013					+		
Duarte et al., 2014	+		+				
Abeln et al., 2015		+	+		+		+
Candido, Okuno, da Silva, Machado, & Nakamura, 2015				+			
Gutmann et al., 2015		+	+*				+
Robertson & Marino, 2015		+			+		
Edwards, Deakin, & Guy, 2016			+*		+		
Cruz et al., 2017				+		+	
da Silva et al., 2017	+			+			
Michael, Graham, & Davis, 2017				+		+	
Gutmann et al., 2018		+	+*				+
Shiraishi et al., 2018	+			+		+	
Dykstra, Hanson, & Miller, 2019			+		+		
di Fronso et al., 2019		+					+
Maceri & Cherup, 2019		+	+		+		

Chronologically ordered GXT research with analyzed RPE, HRV or EEG – left column, Pre-GXT – signify analyzed parameters before GXT conduction, During-GXT – signify analyzed parameters during GXT conduction, Post-GXT – signify analyzed parameters after GXT conduction, + analyzed parameters, * only once immediate after GXT termination.

Referring to the neurophysiological area, all studies collectively revealed an increase of brain activity power in the measured brain lobes as a consequence to GXT execution, despite some methodological differences. These differences are in e.g. GXT design, brain activity analysis, measured frequency bands (e.g. delta, theta, alpha, beta or gamma (only analyzed by (Robertson and Marino, 2015) and defined with 30-40 Hz frequency) and brain lobes (e.g. frontopolar, frontal, central, temporal, parietal or occipital lobe). Further studies (Dykstra et al., 2019; Mechau et al., 1998; Robertson and Marino, 2015) reported a decline of brain activity over the whole cortex, especially in the temporal and prefrontal cortex (PFC) at high intensities. Although several studies provided evidence for common tendencies, a concrete reproduction of results is according to the methodological differences (e.g. selection and time duration of GXT stages used for analysis) hardly to be identified. In addition, individual differences in the conducted GXT duration and performance were mostly neglected. Other studies revealed changes in the current density of the primary motor cortex (Brümmer et al., 2011) and the PFC (Abeln et al., 2015) with a direct relation to exercise intensity. Also a moderate positive correlation between PFC activity and heart rate (HR) was found (Abeln et al., 2015). Rest analysis after GXT was only investigated by two studies (Bailey et al., 2008; Mechau et al., 1998). Therein, pre-exercise level of general brain activity was reached after ten (Bailey et al., 2008) and fifteen minutes (Mechau et al., 1998). Regarding iAPF analysis, studies showed an increase of iAPF after GXT termination (di Fronso et al., 2019) with a prolonged effect until 10 minutes after exercise cessation (Gutmann et al., 2015; Gutmann et al., 2018) proposing an ANS regulation (di Fronso et al., 2019) and an improvement of perceptual and cognitive performance (Gutmann et al., 2018). In spite of some differences in EEG results, the majority of the studies suggest the brain activity manifestation most probably relies on peripheral physiology or central brain mechanism.

With respect to the area of psycho-behavioral measures, one study reported a strong increase of RPE from beginning to termination of the GXT (Faulkner and Eston, 2007) indicating high subjective perceived exertion probably as a consequence to cardiovascular exhaustion. Hereby, other potentially RPE influencing factors such as the core affect (di Fronso et al., 2020) or the focus of attention (Lohse and Sherwood, 2011) should be kept in mind. Concerning a connection to the neurophysiological system, a self-paced GXT study, regulated by RPE evaluation, examined a link of RPE to brain activity (Maceri and Cherup, 2019). In all measured parameters, an increase of prefrontal and central alpha as well as beta power was examined as a consequence to exercise conduction (Maceri and Cherup, 2019). Increased beta power in the prefrontal cortex (PFC) and motor cortex (MC) was explained to rely on a higher demand of planning and execution of movement during a GXT. Alpha power was linked to afferent feedback signaling regulated by PFC and also related to inhibited MC (Maceri and Cherup, 2019; Robertson and Marino, 2015).

For a comprehensive view of all three areas containing mostly effects that have been analyzed separately and were caused by exercise, this study aims to investigate the neurophysiological and cardiovascular as well as subjectively perceived strain of an exhaustive task by means of a GXT and their possible interactions in parallel. Therefore, not only the influence of a GXT on EEG brain activity, on RPE as well as on HRV is analyzed by comparing passive resting states prior and immediately after the GXT, but also during the exercise and in passive short-term recovery. According to the general statement of the presented state of research, we hypothesize an increase of brain activity (power of total spectrum and frequency bands: theta, alpha, beta, gamma) distributed over the whole cortex (temporal, parietal, occipital, particularly (pre)frontal and central lobe) as well as of iAPF, from baseline rest until rest directly after exhaustion. In contrast, HRV (LF and HF power) is expected to strongly decrease from beginning till exhaustion. RPE is assumed to strongly increase until GXT termination. Regarding recovery, we speculate a decreasing brain activity (power of total spectrum and frequency bands: theta, alpha, beta, gamma) over the whole cortex ((pre-)frontal, central, temporal, parietal, occipital lobe) and decreasing RPE, but an increasing HRV (LF and HF power) in direction to pre-exercise level (Kaikkonen et al., 2008). We also put forward the hypothesis of a negative correlation between brain activity (power of total spectrum and frequency bands: theta, alpha, beta, gamma) and HRV (LF and HF power) and hypothesize about a direct relationship of brain activity (power of total spectrum and frequency bands: theta, alpha, beta, gamma) and RPE.

Methods

Participants

Fifteen healthy male volunteers (23.6 ± 2.7 years; 1.83 ± 0.07 m; 78.6 ± 8.9 kg) participated in this study. Based on the aspect that independent of sample size no generalization of the hypothesis to the population can be conducted, the applied sample size is sufficient to provide, according to Fisher's statistics, results with enough basis to potentially foster research of similar studies (Gigerenzer, 2004; Nuzzo, 2014; Stegmüller, 1973). Only male participants with an age between 19 and 28 were recruited in order to control gender and age dependent effects on the brain (Wackermann and Matousek, 1998; Wada et al., 1994) and heart activity (Kuo et al., 1999; Umetani et al., 1998). All participants fit the neurologically necessary condition of the same handedness to compare brain activity (Serrien et al., 2006; T. Sun and Walsh, 2006). Right-handedness was selected as a criterion for study participation to facilitate acquisition of possible participants. Volunteers classified themselves as neurologically and cardiologically healthy and mentioned no related medical pre-existing conditions. Physical or cerebral activity influencing substances (Zschocke and Hansen, 2012), like coffee, alcohol or medication, have not been consumed at least 24 hours before the measurement. Subjects gave their written informed consent for study participation. None of the participants had prior experience of an incremental exercise test, but estimated to be able to perform a GXT. The process of a GXT was explained to the subjects before study beginning.

Participants were coded with numbers for anonymity of personal data. Table 2 gives an overview of the included demographic and lifestyle variables. Compliance with the ethical standards took place under the conditions of the local institutional ethics committee. The study has been carried out in accordance with the Declaration of Helsinki (2013).

Table 2. Questionnaire of demographic and lifestyle variables.

Variables		Type of evaluation
Gender		male / female
Birthdate		month & year
Height		_______ cm
Weight		_______ kg
Neurological impairment		yes / no
Cardiological impairment		yes / no
Right-handedness		yes / no
Experience in a graded exercise test		yes / no
Ability to perform a graded exercise test		yes / no
Dependent of experiment day (last 24h):		
Alcohol consumption	yes / no,	if yes, how much?
Medication	yes / no,	if yes, kind and dosage
Coffee	yes / no,	if yes, how much?

Variables used to evaluate participants demographic and lifestyle facts.

Study design and procedure

The study was conducted at the Sports Institute of the Johannes Gutenberg University of Mainz. With a within-subject design the effects of a GXT were investigated. EEG brain activity and ECG HRV as well as the Borg scale of perceived exertion (RPE) (Borg, 1982) were chosen as measurement parameters for (neuro-)physiological and subjectively perceived stress. Additionally, the grade of wellbeing, concentration and sleep was assessed via a classification of good, moderate or bad. The measurements were carried out under laboratory conditions. Changes in brightness and ambient noise were kept to a minimum and temperature was standardized (mean 21.2 SD 0.8°C).

The measurement procedure (Figure 1) started by identifying the current subjective state of every participant by means of the grade of wellbeing, concentration and last night's sleep. Subsequently, at rest a measurement of spontaneous EEG activity with eyes open and ECG heart activity was conducted for five minutes just before the beginning of warming up for GXT. Subjects warmed up at 25W for three minutes. The GXT protocol was carried out on an individually adapted cycle ergometer until exhaustion under measurement of EEG and ECG activity as well as perceived exertion. Immediately afterwards, the recovery process was assessed sitting on a chair during 15 minutes with EEG brain and ECG heart activity measurement. Perceived exertion was rated after each increase of physical load and directly at exhaustion. Measurements before and after the GXT were conducted sitting on an immobile chair with eyes open and watching a smiley picture, fixed on head height in a few meters distance on the wall. Subjects were asked to sit comfortably, but also to minimize their head and eye movements.

Graded exercise test

The graded exercise test was performed on the electromagnetically bicycle ergometer (Lode Excalibur - Lode B.V., Groningen, Netherlands). The protocol started with a resistance of 50W and an increase of 50W every 3 minutes until exhaustion (Huonker, 2004). Cycling cadence was prescribed with 60-70 rpm. Subjects were asked to keep movements of upper body and head to a minimum. Eyes were directed forward towards a smiley picture which was attached to the wall three meters away, at head height. Potential movement artefacts were tried to be restricted to a minimum. On the one hand the effects of seated cycling as an exercise with few vertical as well as horizontal whole-body movements were investigated. On the other, several methods of data cleansing were applied. The test was terminated by the second violation of the cadence interval, i.e. cadence below 60 rpm was only tolerated a single time. Furthermore the occurrence of exhaustion as well as stopping criteria (Dickhuth and Badtke, 2010) led to a termination of the GXT. No type of external motivation was given in order to prevent enhancing a subjects' willpower, which could extend its stamina and result in a longer test duration till GXT termination.

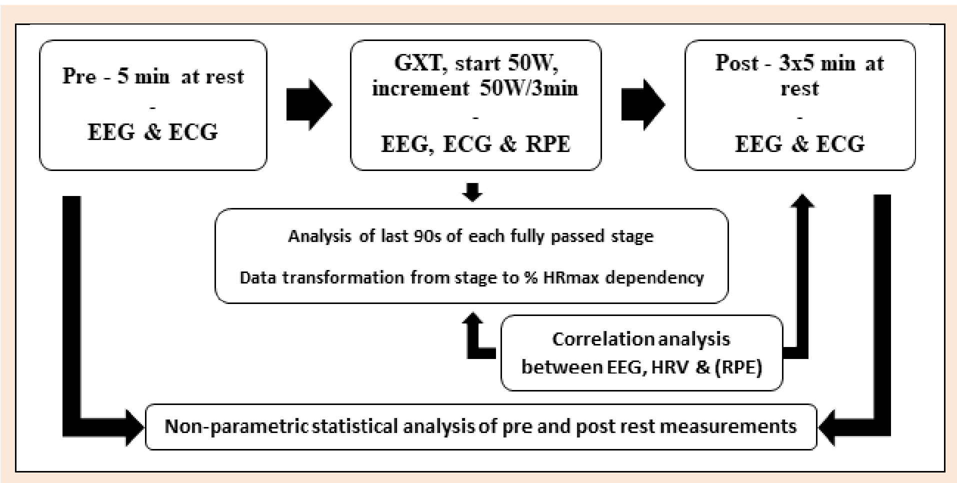

Figure 1. Test procedure and overview of data processing and analysis. Boxes at the top present the test procedure with type of measurement conducted. Boxes below describe the type of analysis. Correlation analysis was conducted between EEG, HRV and RPE data during the GXT as well as of recovery.

Borg scale of perceived exertion

The Borg rating of perceived exertion scale (RPE) (Borg, 1982) was applied to evaluate the exertion level during each stage of the GXT. At the end of every stage as well as at GXT termination subjects were asked to give their individual RPE shortly. Subjects read an instruction of RPE one day and directly prior to the measurement beginning to ensure reliable exertion output. A RPE of 6 was defined as no effort at all and a RPE of 20 as maximum effort ever experienced.

Electroencephalography

Spontaneous EEG was assessed during the whole test procedure by means of the EEG-system Micromed SD LTM 32 BS (Venice, Italy) with a sampling rate of 1024 Hz and recorded by the international 10-20 system using 19 electrodes, including Fp1, Fp2, F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, T6, O1 and O2. EEG was recorded before and after the GXT at rest as well as during the exercise. For all EEG measurements a homogeneous and low impedance (<10kOhm) of the electrodes in all points was sought. The conduction of brain activity was unipolar with grounding on the nose. Furthermore, a two channel electrooculogram with electrodes at the medial upper and lateral orbital rim of the right eye was applied. Data was recorded by means of commercially available software (SystemPlus Evolution - Micromed, Venice, Italy).

Electrocardiography

ECG was assessed by means of an additional bipolar channel of the EEG-system Micromed SD LTM 32 BS with a sampling rate of 1024 Hz and recorded by the second lead according to Einthoven. One electrode of the second Einthoven limb lead was placed on the right side of the body, lateral, directly below the clavicle and the other on the left body side, lateral, directly below the costal arch to reduce artefacts during movement. ECG was recorded during the whole test procedure by means of the software SystemPlus Evolution (Micromed, Venice, Italy). To reduce artefacts as a result of body or ECG cable movement during exercise, the upper body of participants was dressed up with a compressive net tubing.

Data analysis

Throughout the analysis, a statistical significance level of five percent ($p \leq 0.05$) according to Fisher statistics was determined. Calculation of effect size was based on Neyman-Pearson statistics (Neyman and Pearson, 1933) and results were presented by Cohen's d (Cohen, 1988): $d < 0.5$ (small effect), $d < 0.8$ (medium effect), $d > 0.8$ (large effect). According to correlation analysis, the correlation coefficient r was interpreted as followed: $r \geq 0.1$ (small relation), $r \geq 0.3$ (moderate relation), $r \geq 0.5$ (strong relation) (Cohen, 1992). Data of the recorded measurements of brain activity were processed by means of MATLAB-based software EEGLAB 14_1_1b (MathWorks, USA; Swartz Center of Computational Neuroscience, San Diego, USA). Data of ECG, specifically HRV were computed by means of MATLAB-based software Kubios HRV 2.2 (Finland). Data of the recovery process was divided into three five-minute intervals. Processed data and all the other measured data were entered into the software SPSS 23 (IBM, USA) for statistical analysis. All conducted statistical tests were non-parametric to minimize possible influence of artefacts due to body or head movement. Based on rank scaling, the interference of possible outliers in data analysis is reduced (Whitley and Ball, 2002). Data processing and analysis differed between rest and exercise measurements (Figure 1). Descriptive statistics were generated for every sub-region of analysis (Table 3).

Borg scale of perceived exertion and psychological state

Via the correlation of Spearman, an interaction of RPE and EEG as well as HRV parameters during the GXT was analyzed.

The output of the variables general well-being, sleep of the previous night and current concentration were transformed into a frequency scale.

Spectral analysis

A basic finite impulse response (FIR) filter was used to bandpass data (0.1-120 Hz). Furthermore, a notch filter (50 Hz) was applied. For analysis of brain activity recorded during the GXT, only the last 90 seconds of every three-minute stage were taken to minimize possible influence of adaption processes due to the change of load. Spectral analysis was used as assessment and interpretation method of EEG data (Zschocke and Hansen, 2012). Relevant frequency parameters were the theta (4-8 Hz), alpha (8-13 Hz), beta (13-30 Hz), gamma (30-70 Hz) band and the total spectrum (4-70 Hz) (Zschocke and Hansen, 2012). For each frequency band and total spectrum, mean power spectrum of the EEG signal was created by discrete Fast-Fourier-Transformation with a window size of 2 seconds and 75% window-overlap. Interference-prone channels were interpolated. Furthermore, an independent component analysis (ICA) (Makeig et al., 1996) was conducted. Recurring artefacts, such as eye closing, eye movement and muscular artefacts were filtered by reducing interference-prone components. After visual inspection of the complete recordings, individually occurring abnormal interferences of the electric potential, like body movements or sweat artefacts, were eliminated out of the data length. Average data reduction was approximately 10% of each data file length, i.e. 9.5 (SD 5.4) seconds of each data file during the GXT and 30.5 (SD 18.3) seconds of each data file at rest. Power spectrum of the electrodes were averaged across their cerebral areas, i.e. FP1 and FP2 for the frontopolar lobe, F7, F3, Fz, F4 and F8 for the frontal lobe, C3, Cz and C4 for the central lobe, T3, T4, T5 and T6 for the temporal lobe as well as O1 and O2 for the occipital lobe. Furthermore, data of all lobes were averaged to gain information about the total brain power (total power, TP). Average iAPF of all lobes was determined by the mean center of gravity of all channels calculated by an automated iAPF estimation method (Corcoran et al., 2018). For power spectral density estimation via pWelch, a Hamming window with 4 seconds length and 50% overlap was used. The minimum number of channel-estimates necessary for computing cross-channel averages was set to 1. The applied Savitzky-Golay filter for improving spectral peak detection was defined by a frame width of 7 and polynomial

Table 3. Descriptive statistics of significant variables.

			Exhaustion	Post5	Post10	Post15
RPE (6 ≤ x ≤ 20)			18 (1)			
HRV (%)		LF power	0.1 (0.2)	1.7 (2.3)	2.7 (4.1)	4.2 (11.9)
		HF power	0.3 (0.8)	0.4 (1.2)	0.3 (0.8)	0.6 (0.9)
		EDR	195.2 (68.4)	147.8 (49.6)	130 (60.2)	129.6 (43.8)
Brain activity (%)	**Total power**	Total spectrum	106.3 (7.2)	104.8 (15.5)	103.2 (10.3)	104.3 (12.2)
		Theta	102.8 (17.7)	103 (14)	100.8 (8.7)	99.9 (12.1)
		Alpha	104.1 (15.4)	103.6 (12.5)	101.1 (9.3)	102.8 (9.4)
		Beta	104.8 (11.9)	103.8 (14.9)	103.3 (8.3)	102.6 (10)
		Gamma	106.7 (5.4)	105.1 (15.6)	104.6 (11.8)	105.8 (13.7)
	Frontopolar	Total spectrum	109 (23.7)	106 (17.5)	106.5 (22.8)	103.2 (11.1)
		Theta	108 (27.9)	105.1 (15.5)	108 (12.5)	102.2 (12.5)
		Alpha	109 (26.6)	107.8 (13.4)	109.2 (21.3)	106.7 (12.1)
		Beta	104.5 (24.6)	107.6 (17.9)	107.1 (20.7)	103.4 (8.7)
		Gamma	109.4 (20.8)	102.9 (22.8)	106.7 (23.1)	101.3 (15)
	Frontal	Total spectrum	100 (11.2)	104.4 (6.8)	107.7 (13.7)	107.1 (9.9)
		Theta	101.9 (22.6)	103.1 (12.3)	103.5 (10.5)	99.5 (7.3)
		Alpha	101.8 (22.4)	106.2 (10.3)	106.7 (10.4)	104.4 (7.7)
		Beta	99.5 (11.8)	105.4 (8.4)	107.4 (9.9)	103.1 (7)
		Gamma	101.1 (10.6)	105.6 (7.5)	107.8 (16.1)	108.4 (12.9)
	Temporal	Total spectrum	111.1 (15.3)	109.9 (12.9)	105.6 (14.6)	106.7 (11.5)
		Theta	110 (16.2)	107.8 (11.2)	103.8 (12.8)	103.8 (11.3)
		Alpha	109 (15.4)	108.2 (9.9)	105.4 (11.1)	105.8 (10.7)
		Beta	109 (14.7)	108.9 (5.2)	105.9 (13.5)	105.5 (9.3)
		Gamma	110.9 (16.3)	109 (19.4)	106.1 (13.6)	107.8 (13.8)
	Parietal	Total spectrum	107.9 (18.5)	101 (14.9)	98.5 (15.6)	99.8 (13.3)
		Theta	109 (20.3)	99.3 (20.4)	99 (12.8)	96.9 (10)
		Alpha	106 (16.9)	99.3 (18.6)	98.3 (13.4)	99.1 (6.2)
		Beta	103.5 (16.1)	100.5 (16.3)	99.2 (15.1)	100.5 (13)
		Gamma	108.1 (17.4)	100.7 (14.7)	97 (16.5)	100.1 (16.6)
	Occipital	Total spectrum	109 (14.5)	104 (13)	102.3 (14)	102.1 (13.6)
		Theta	108.3 (24.4)	98.7 (12.9)	98.2 (14.2)	98.4 (10.8)
		Alpha	109.9 (25.7)	98.1 (15.1)	99.7 (16.7)	98.2 (11)
		Beta	108.4 (14.4)	101.6 (10.3)	100.1 (14.1)	103.2 (11)
		Gamma	110.5 (18.2)	105.8 (19.6)	100.8 (14.6)	101.9 (16.3)
	iAPF		100.2 (5.8) [2]	100.1 (3.7) [1]	100.9 (5.6) [1]	100.6 (2.7) [1]

Columns defined by measurement times, rows defined by selected variables of RPE, HRV and brain activity. Brain activity divided by cerebral lobes and subdivided by frequency bands, mean power spectrum of total spectrum (4-70 Hz), theta (4-8 Hz), alpha (8-13 Hz), beta (13-30 Hz) and gamma (30-70 Hz) frequency. Exhaustion values normalized to first stage of GXT (%50W), Post5-15 values normalized to pre-rest (%Pre). Median (IQR) values, [1] only including 14 subjects and [2] only including 13 subjects according to failed iAPF detection.

order of 5. EEG data of rest measurements was normalized by defining Pre-values as baseline (100%) and presenting post-rest values relative to Pre-values (%Pre) by dividing the specific Post- through Pre-values. According to different data length between data of recovery and GXT, data during the exercise was normalized to the first stage of the GXT (50W) and expressed as a relative (%50W) by dividing each GXT stage value through the 50W-value. As a consequence, data of 50W, i.e. presenting 100% of %50W, was excluded from correlation analysis. To minimize the influence of noise and according to a rather small number of measurements, the median was used for further analysis of spectral power.

For statistical examination, the Friedman test including Dunn-Bonferroni tests for post hoc analysis (comparison of rest measurements), as well as Spearman correlation were used due to nonparametric data and to reduce the effect of possible outlier measurement data. To determine a possible interaction between brain activity and HRV parameters as well as RPE, several correlations with differing measurement data were conducted. One correlation analysis included data only measured during the GXT (data of the completed GXT stages transformed in dependency of relative HRmax) and the other was only related to data of the recovery process (Post5, Post10, Post15 data).

HRV analysis

HRV-data was bandpass filtered by a basic FIR filter (0.1-120 Hz) as well as notch filtered (50 Hz). HRV was used as assessment and interpretation method of ECG data. For analysis the second lead (electrode below the right clavicle to electrode below the left costal arch) of the Einthoven triangle was used according to most clear signal characteristics and least artefacts. Via Kubios HRV, ECG data was inserted and computed for the time intervals of the test procedure. First, correct RR detection was proofed via visual inspection of ECG raw signal and incorrect or missing detection was adjusted. Artefact correction tool was used to eliminate artefacts of RR data. Over all measurements, artefact reduction was <10% of total data. Detrending of RR data was conducted applying the method Smooth Priors with λ = 380, resulting in a cut-off frequency of 0.040 Hz (Tarvainen et al., 2002). Frequency analysis was calculated via Fast Fourier Transformation with Welch's periodogram method and interpolation rate of 4 Hz, window-width of 120 s and window-overlap of 75% for rest measurements and window-width of 40 s and window-overlap of 75% for GXT data. HRV data of rest measurements was normalized by defining Pre-values as baseline and presenting post-rest values relative to Pre-data (%Pre). According to different data length between data of recovery and GXT, data during the exercise was normalized to the first stage of the GXT (50W) and expressed as a relative (%50W).

Time domain (Mean RR, Mean HR, SDNN, RMSSD), frequency domain of low frequency (LF, 0.04-0.15 Hz) and high frequency (HF, 0.15-0.4 Hz) power (Shaffer and Ginsberg, 2017) as well as ECG derived respiration (EDR) (Cysarz et al., 2008) were analyzed. Mean RR is defined as the arithmetic mean of the time between two consecutive R-peaks of the ECG signal. SDNN, standard deviation of normal sinus beat intervals, is an indicator of sympathetic (SNS) and parasympathetic nervous system (PNS) activity. It correlates with LF power (Umetani et al., 1998). RMSSD stands for root mean square of successive differences between normal heartbeats and informs about the beat-to-beat variance in HR and is typically taken for the evaluation of the PNS influence on HRV changes. It correlates with HF power (Kleiger et al., 2005). LF power is defined as the power of HRV-activity with a frequency of 0.04 to 0.15 Hz and is mainly associated with the activity of the SNS and PNS. HF power reflects primarily the PNS activity. EDR represents an easy applicable estimate of respiratory frequency, particularly reliable in context with higher levels of physical activity (Cysarz et al., 2008). With information about the respiratory rate, interpretation of ANS regulation, specially HF power changes may be facilitated (Cysarz et al., 2008).

To facilitate the presentation of results and minimize the amount of calculated HRV parameters, a principal component analysis was conducted. Additionally, the knowledge about existing correlations between several HRV parameters helped to focus on the most relevant HRV parameters. Thus, presentation of HRV parameters was reduced to LF power, HF power and EDR.

The Friedman test including Dunn-Bonferroni tests for post hoc analysis was applied for statistical examination of effects between rest measurements. Via the correlation of Spearman, HRV and EEG parameters were analyzed for linear interactions during post-rest measurements and furthermore during the GXT. To normalize subject dependent, different performance level and time of the GXT, maximal heart rate (HRmax) of each subject was determined and mean HR of each stage was represented as a relative of the HRmax. Hence, all other HRV as well as EEG and RPE parameters were presented in dependency of relative HRmax. This data processing was also conducted with the data of recovery.

Results

Table 3 displays the descriptive results of selected variables.

Psychological state

Before starting the experiment, grade of well-being was rated in 87% of the cases as good and 13% as moderate. Last night's sleep was evaluated nearly equally distributed between moderate 53% and good 47%. Subjects declared to 80% a good and to 20% a moderate ability to concentrate.

Spectral analysis

Statistical analysis revealed EEG frequency band dependent effects in pre- to post-rest comparison (Table 4). In the total spectrum and in each frequency band, there was a global significant effect in the temporal lobe. Post hoc analysis identified significant effects between pre- (Pre) to the first post-rest (Post5) and between pre- and the second post-rest (Post10) measurement in the temporal lobe. Additionally, alpha, beta and gamma frequency bands showed significant effects in comparison of the pre- and the last post-rest measurement (Post15). In the frontopolar lobe, theta, alpha and beta frequency was significantly different over all rest measurements and in post hoc-test comparing Pre and Post5. Only in alpha and beta frequency, post hoc comparison of Pre and Post10 led to significant effects. According to the frontal lobe, there were global significant effects in the alpha and beta frequency band, but only alpha frequency showed significant effects in post hoc comparison of Pre to Post5 and Post10. Regarding iAPF analysis, 135 out of 139 possible iAPF estimations could be extracted in accordance with the detection criteria (Corcoran et al., 2018). This resulted in an exclusion of maximal two subjects in the calculation of descriptive and inference statistics (comparison of pre- and post-rest measurements). Analyzing the pre- and post-rest measurements led to no significant difference in iAPF.

HRV analysis

Statistical analysis of HRV revealed global significant effects in all parameters in pre- to post-test comparison (Table 5). Post hoc analysis led to parameter dependent differences. Related to LF power, there were significant effects between Pre and Post5 as well as Post10, and between Post5 and Post15. HF power showed significant effects from Pre to each post-rest measurement. EDR significantly differed between Pre and Post5.

Correlation of EEG power spectrum, HRV, and RPE

To investigate a possible relationship of EEG, HRV, and RPE parameters, correlation analysis of the different data sources was calculated during the exercise as well as during recovery. Correlation analysis revealed an EEG frequency band and location dependent relation between power spectrum and HRV as well as RPE (Table 6-7). According to increasing load, there were related changes of the main measured parameters (Figure 2).

Furthermore, correlation analysis of data during the GXT (Table 6) resulted in mainly moderate negative effects of total spectrum and beta as well as gamma frequency in total power and the frontopolar, temporal and occipital lobe with LF power (Figure 3). Regarding a correlation with HF power, the total power and the occipital lobe showed moderate negative correlations in beta and gamma frequency as well as total spectrum.

Table 4. Significant time effects of EEG power spectrum in pre- and post-exercise comparison.

		df	χ^2	p	Post hoc	Z	p	d
Frontopolar	Theta	3	9.72	.021	Pre-Post5	-1.333	.028	.733
	Alpha	3	10.28	.016	Pre-Post5	-1.267	.043	.692
					Pre-Post10	-1.333	.028	.733
	Beta	3	12.52	.006	Pre-Post5	-1.533	.007	.862
					Pre-Post10	-1.333	.028	.733
Frontal	Alpha	3	13	.005	Pre-Post5	-1.400	.018	.775
					Pre-Post10	-1.533	.007	.862
	Beta	3	7.8	.05				
Temporal	Total spectrum	3	18.68	< .001	Pre-Post5	-1.733	.001	1.001
					Pre-Post10	-1.733	.001	1.001
	Theta	3	11.08	.011	Pre-Post5	-2.687	.043	.692
					Pre-Post10	-2.970	.018	.775
	Alpha	3	15.08	.002	Pre-Post5	-1.600	.004	.907
					Pre-Post10	-1.533	.007	.862
					Pre-Post15	-1.267	.043	.692
	Beta	3	19.56	< .001	Pre-Post5	-1.800	.001	1.05
					Pre-Post10	-1.800	.001	1.05
					Pre-Post15	-1.333	.028	.733
	Gamma	3	16.68	.001	Pre-Post5	-1.600	.004	.907
					Pre-Post10	-1.667	.002	.954
					Pre-Post15	-1.400	.018	.775

Rows defined by cerebral lobes, each divided by frequency bands, total spectrum (4-70 Hz), theta (4-8 Hz), alpha (8-13 Hz), beta (13-30 Hz), gamma (30-70 Hz). Global results – left column, post hoc-test via Dunn-Bonferroni – right column.

Table 5. Significant time effects of HRV parameters in pre- and post-exercise comparison.

	df	χ^2	p	Post hoc	Z	p	d
LF power	3	35	< .001	Pre-Post5	2.533	< .001	1.729
				Pre-Post10	2.133	< .001	1.32
				Post5-Post15	-1.467	.011	.819
HF power	3	28.28	< .001	Pre-Post5	2	< .001	1.206
				Pre-Post10	2.267	< .001	1.444
				Pre-Post15	1.733	.001	1.001
EDR	3	9.48	.024	Pre-Post5	-1.4	.018	.775

Rows defined by HRV parameters. Global results – left column, post hoc-test via Dunn-Bonferroni – right column.

Considering RPE and EDR, only temporal gamma power led to a moderate positive correlation (Figure 3). iAPF revealed no moderate correlation to HRV parameters and RPE, but in relation to specific brain frequency bands. A moderate negative correlation of iAPF with theta and alpha frequency in the frontal, central lobe as well as in the total power and a moderate positive correlation of the temporal gamma activity was identified (Figure 4).

Concerning the recovery after the GXT, there were clearly fewer moderate correlations between brain activity and HRV (Table 7). Solely, temporal power of the total spectrum, beta and gamma frequency revealed moderate negative correlations with HF power (Figure 5). The iAPF only correlated moderately negative with frontal theta power (Figure 4).

Discussion

This study aimed to investigate the effects of an exhaustive physiological demand on the (neuro-) physiological system as well as the subjectively perceived exertion and their interaction. The influence of a GXT, performed on a cycle ergometer, on EEG brain activity, HRV as well as RPE was analyzed by comparing resting states prior and directly after the exercise and by correlation analysis during the exercise and in short term recovery. According to the state of research, we hypothesized an increase of brain activity (power of total spectrum and frequency bands: theta, alpha, beta, gamma) over the whole cortex (temporal, parietal, occipital lobe, particularly (pre)frontal and central lobe) from baseline rest to rest directly after exhaustion. HRV (LF and HF power) was expected to strongly decrease from beginning until exhaustion. RPE was assumed to strongly increase during the GXT. Referring to the recovery process, it was speculated that total brain activity (all measured frequency bands in all lobes) decreases and HRV (LF and HF power) increases in direction to pre-exercise level. With regard to a correlation analysis, we hypothesized an inverse relation of total brain activity and HRV as well as a positive relation of total brain activity to RPE. The correlation analysis was conducted with data measured during the GXT and with data measured during the recovery process. The results comparing pre- and post-exercise rest measurements are discussed prior to the results during the GXT.

Comparison of pre- and post-exercise rest measurements

Concerning HRV, there were highly significant global effects of all frequency parameters as well as a significant global effect in EDR in comparison to rest measurements.

Table 6. Correlations between EEG power spectrum and HRV/RPE parameters during exercise.

Frequency		LF power	HF power	EDR	RPE	iAPF
Total power	Total spectrum	**-.392**	**-.323**	.178	.135	.006
	Theta	-.245	-.157	.028	-.043	**-.311**
	Alpha	-.234	-.142	-.058	-.071	**-.342**
	Beta	**-.329**	**-.302**	.131	.071	-.035
	Gamma	**-.395**	**-.318**	.207	.202	.123
Frontopolar	Total spectrum	-.295	-.184	.074	.085	-.079
	Theta	-.283	-.137	.013	.017	-.25
	Alpha	-.261	-.148	-.046	-.005	-.242
	Beta	-.278	-.179	.047	.047	-.104
	Gamma	**-.334**	-.209	.114	.134	-.003
Frontal	Total spectrum	-.208	-.128	.154	.035	-.158
	Theta	-.159	-.07	.025	-.081	**-.303**
	Alpha	-.163	-.063	-.045	-.097	**-.36**
	Beta	-.173	-.118	.109	-.009	-.167
	Gamma	-.217	-.149	.23	.095	-.081
Temporal	Total spectrum	**-.403**	-.266	.282	.275	.233
	Theta	-.270	-.142	.059	.006	-.174
	Alpha	**-.322**	-.173	.012	.015	-.178
	Beta	**-.394**	-.276	.266	.233	.205
	Gamma	**-.377**	-.253	**.307**	**.312**	**.307**
Central	Total spectrum	.017	-.03	.145	.067	-.076
	Theta	-.058	-.04	.04	-.042	**-.365**
	Alpha	.002	.001	-.057	-.087	**-.425**
	Beta	0	-.053	.116	.012	-.138
	Gamma	-.004	-.054	.224	.175	.053
Parietal	Total spectrum	-.171	-.169	-.012	-.073	-.071
	Theta	-.141	-.051	-.124	-.226	-.272
	Alpha	-.08	.009	-.185	-.266	-.287
	Beta	-.132	-.147	-.058	-.133	-.093
	Gamma	-.21	-.203	.059	.032	-.006
Occipital	Total spectrum	**-.386**	**-.388**	.072	.149	.125
	Theta	-.270	-.251	-.045	-.01	-.165
	Alpha	-.22	-.21	-.119	-.043	-.139
	Beta	**-.383**	**-.390**	.069	.126	.114
	Gamma	**-.396**	**-.392**	.110	.196	.190
iAPF		-.209	-.214	.14	.247	

Rows defined by cerebral lobes, each divided by frequency bands, total spectrum (4-70 Hz), theta (4-8 Hz), alpha (8-13 Hz), beta (13-30 Hz), gamma (30-70 Hz). Correlation coefficient r values, moderate and strong correlations in bold.

As expected by earlier research (Banach et al., 2004), LF and HF power of post hoc analysis highly significantly decreased as a consequence of the GXT, i.e. pre- to first post-rest comparison (Pre-Post5). In the same context, EDR led to a significant increase indicating a raised respiratory rate. Thus, the existence of strong physiological strain and a connected regulation of the ANS evoked by the GXT can be assumed.

Regarding brain activity, the analysis of all rest measurements (Pre, Post5-Post15) revealed a global significant effect of EEG power in total and in each frequency band in the temporal lobe. Frontopolar, there were significant global effects in the theta, alpha and beta band, but not in gamma. Alpha and beta activity differed in general significantly in the frontal lobe. Referring to iAPF analysis, no significant global effect was determined. This result is in contrast to significant increased iAPF after an exhausting task examined by other studies (Gutmann et al., 2015; Gutmann et al., 2018). But our results show a similar trend, i.e. a slight increase after the GXT and further increase till 10 minutes of recovery. According to present interindividual differences in iAPF (Mierau et al., 2017), differing results could be based on a missing baseline normalization in the other studies. Concerning the acute effect of GXT (comparison of Pre and Post5), post hoc analysis showed a significant increase in the whole temporal spectrum, in frontopolar theta, alpha and beta power as well as frontal alpha power. No significant changes either in the total spectrum power or in the central, parietal and occipital lobes were found. Thus, the assumption and hypothesis of an overall power increase (Bailey et al., 2008; Mechau et al., 1998; Robertson and Marino, 2015) could not be confirmed with the data underlying this study. Thus, a frequency and lobe specific interpretation of results was indicated. But, referring to the applied EEG system and analysis method, an interpretation that is specific to brain areas has to be handled with caution in general (Michel and Brunet, 2019). The significant increase of temporal total spectrum was not observed so far by other GXT studies. Only one study (Mechau et al., 1998) described changes in the temporal lobe, but only a reduction of beta and alpha1 power in the shift from moderate to high intensity load. Also, temporal power changes were unexpected due to the absence of any acoustical or other sensory motivation stimuli. However, this change could point to raised working memory processes (Malik and Amin, 2017), increased attention as well as multisensory and sensorimotor integration (Jensen et al., 2007). Conducting a physical activity,

Table 7. Correlations between EEG power spectrum and HRV parameters in recovery.

Frequency		LF power	HF power	EDR	iAPF
Total power	Total spectrum	.012	-.214	.04	-.027
	Theta	.053	-.181	.057	-.116
	Alpha	.052	-.152	.048	-.065
	Beta	-.06	-.26	.036	0
	Gamma	.026	-.223	.037	-.022
Frontopolar	Total spectrum	-.085	-.123	.15	-.209
	Theta	-.105	-.171	.069	-.182
	Alpha	-.072	-.091	.014	-.187
	Beta	-.108	-.118	.14	-.205
	Gamma	-.091	-.133	.16	-.182
Frontal	Total spectrum	.062	-.056	.017	-.181
	Theta	.056	-.072	.087	**-.309**
	Alpha	-.055	-.174	.088	-.219
	Beta	-.014	-.129	.089	-.198
	Gamma	.092	.003	-.019	-.15
Temporal	Total spectrum	-.086	**-.338**	.179	-.011
	Theta	.039	-.207	.152	-.061
	Alpha	.104	-.176	.129	-.054
	Beta	-.063	**-.310**	.174	.005
	Gamma	-.088	**-.349**	.172	-.017
Central	Total spectrum	.019	-.134	-.105	.217
	Theta	.08	-.109	-.087	.162
	Alpha	.101	-.069	-.052	.145
	Beta	-.017	-.172	-.089	.239
	Gamma	.012	-.115	-.104	.205
Parietal	Total spectrum	-.062	-.227	-.007	.133
	Theta	-.005	-.177	.076	-.011
	Alpha	-.058	-.206	.093	.067
	Beta	-.114	-.299	.024	.118
	Gamma	-.071	-.225	-.029	.142
Occipital	Total spectrum	.081	-.152	-.04	.006
	Theta	.132	-.092	-.023	-.061
	Alpha	.021	-.179	-.043	.028
	Beta	-.012	-.218	-.04	-.009
	Gamma	.09	-.135	-.036	-.017
iAPF		-.177	-.101	-.266	

Rows defined by cerebral lobes, each divided by frequency bands, total spectrum (4-70 Hz), theta (4-8 Hz), alpha (8-13 Hz), beta (13-30 Hz), gamma (30-70 Hz). Correlation coefficient r values, moderate and strong correlations in bold.

e.g. from low intensity to exhaustion, may require a permanent processing of differing sensory stimuli sent from the inner body (e.g. ANS, muscular system, psychological system) and from the environment (e.g. control of cadence compliance) (Davranche et al., 2015; Furley and Wood, 2016; Kayser, 2003; McMorris et al., 2015; Tomporowski, 2003). Concerning working memory, medial temporal lying hippocampus with its memory related functions may have been provoked through physical exercise (Voss et al., 2020). Additionally, higher working memory was identified after physical exercise (Tsujii et al., 2013; Voss et al., 2020), particularly at higher intensity (Chang et al., 2013). Relating to the Working Memory Model (Baddeley, 2000), the Central Executive may be demanded to regulate attention to the incoming important stimuli and to disregard others. Furthermore, the provoked temporal power could be evidence for possibly provoked emotional processes in the inner temporal lobe lying amygdala (Kolb and Whishaw, 2009; Ray and Cole, 1985), in context to a GXT execution like ambition, mental fortitude or perseverance. Here of, increased amygdala activation was examined as a consequence of increased exercise intensity (Robertson and Marino, 2016). Furthermore, activation of the amygdala seems to rely on the PFC inhibiting visceral interoceptive responses associated with HRV (Sakaki et al., 2016). The increase of frontopolar and frontal activity could suggest a provoked PFC. Related to the frontopolar lobe, top-down control of executive functions like selective attention, self-control and -regulation could be provoked as a consequence of maintaining goal-directed behavior as demanded by a GXT execution (Robertson and Marino, 2015). Additionally, the prefrontal cortex is most often linked with the control of emotional behavior and basic drives essential for fundamental viability like hunger, thirst, but also physical activity (Fuster, 2001). The revealed higher frontopolar beta power is in accordance with prior studies (Moraes et al., 2007; Robertson and Marino, 2015). The increase of beta power could be interpreted as higher cortical activation (Cheron et al., 2016; Moraes et al., 2007) and augmented arousal level (Abhang et al., 2016) as well as indicating an enhanced attentional demand (Nielsen and Nybo, 2003). The increment in frontopolar theta activity could support the assumption of increased top-down control of executive functions as a consequence of GXT conduction (Cavanagh and Frank, 2014; Robertson and Marino, 2015). The increased frontopolar and frontal alpha power is comparable to prior results (Bailey et al., 2008; Edwards et al., 2016; Mechau et al., 1998; Robertson and Marino, 2015). Frontal alpha power seems to promote information processing (Robertson and Marino, 2015) and be related to enhanced internal mental activity (Stein and Sarnthein, 2000) as well as attention (Cheron et al., 2016).

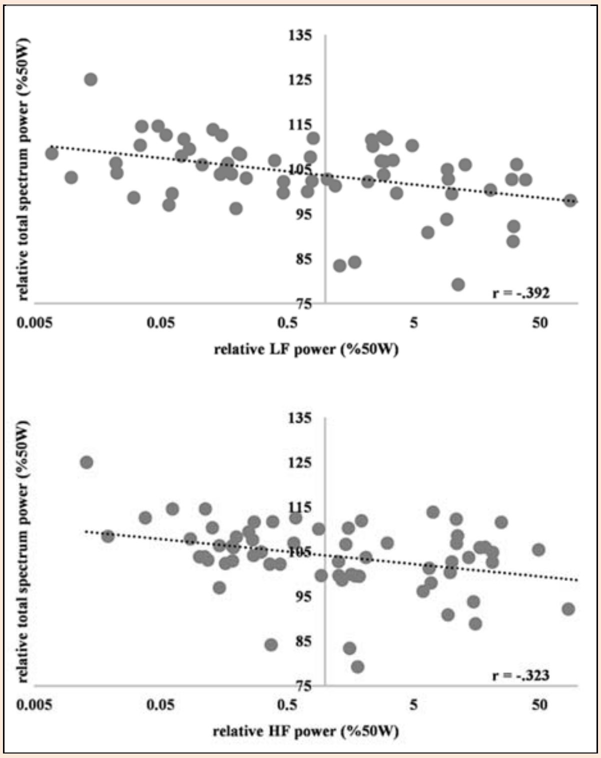

Figure 2. Correlations of total spectrum power and HRV parameters during GXT. GXT data normalized to 50W-values and presented as %50W, data of 50W excluded. LF and HF power plots with log-10 scale, r Spearman's rank correlation coefficient.

In view of the recovery process, a noteworthy cardiovascular recuperation after the GXT was confirmed due to increasing frequency-domain parameters dependent on recovery duration. Supporting this, LF power showed also a significant difference between the first and last post-rest measurement (Post5-Post15). Regarding the comparison to pre-rest, highly significant reductions in LF and HF power were calculated up to ten minutes after GXT termination (Pre-Post10). 15 minutes after exhaustion, only HF power stayed significantly reduced to pre-rest condition. EDR only showed a significant increment until Post5. Therefore, a probably prolonged blocked parasympathetic activity independent of respiratory rate as a consequence of exhaustion is hypothesized. In contrast to HRV, EEG power analysis of recovery showed a mostly decreasing trend, but without a significant effect on brain activity between post-rest measurements. Compared to pre-rest, significant differences in all above mentioned global EEG effects up to 10 minutes after exhaustion (Pre-Post10) were revealed. 15 minutes after exhaustion, only temporal alpha, beta and gamma frequency stayed significantly different from baseline. This could be interpreted as still provoked attention and working memory processes as well as existing emotional processes supporting the hypothesis of an enormous (neuro-)physiological strain and somatosensory demand (Herrmann et al., 2010) due to a GXT. Comparing the recovery process of HRV and brain activity, pre-exercise level of HRV parameters were far from being reached during 15 minutes of recovery. EEG results point towards almost complete recovery indicating a probably shorter recuperation time of brain activity than of the ANS. Referring to the still prolonged influence on HF power of HRV and temporal lobe EEG-activity, a possible reciprocal connection could be implied.

Correlation analysis during GXT and in recovery

To support the hypothesis of a negative relationship between total EEG spectral power and HRV (LF and HF power), correlation analysis was used in one case of data measured during the GXT and in another case of data measured during the recovery process. To facilitate the interpretation of results, only at least moderate correlations are discussed. Correlation analysis during the GXT revealed moderate effects of total spectrum power with LF and HF power, but validity of results could be impaired according to a possible impact of pooled data. Nevertheless, these results of total power could support the hypothesis that through exercise induced widespread changes in EEG brain activity are caused by peripheral physiology (Kraaier et al., 1988; Kraaier et al., 1992) and metabolism processes (Mechau et al., 1998). Regarding the correlation analysis in greater detail, next to the total spectrum particularly higher frequencies such as beta and gamma activity registered mostly the highest correlation effects with HRV parameters. Beta frequency is suggested to play a central role in the processing of sensorimotor information (Cheron et al., 2016) and be provoked at increasing emotional arousal (Aftanas and Golocheikine, 2001). The presence of both aspects could be suggested as a consequence of an exhausting exercise. A link of beta frequency with cardiovascular strain, as the correlation effects indicate, could be supposed. Referring to gamma frequency, a direct connection of somatosensory demand to cardiovascular strain may be existent. Brain lobe specific, LF power correlated moderately negative with the frontopolar, temporal and occipital lobe. Furthermore, the total power as well as the occipital lobe showed mostly moderate negative effects with HF power. In context with EDR and RPE, solely temporal gamma activity led to a moderately positive effect. The moderate negative correlation between LF power and frontopolar gamma power hypothesize that the level of working memory (Jensen et al., 2007) and attention processes (Herrmann et al., 2010) in context with executive functions are directly connected with a regulation of the ANS. Additionally, PFC related top-down control of executive functions, provoked by physical exercise (Robertson and Marino, 2015), seems to increase with higher physiological demand. Furthermore, the PFC linked regulation of emotional behavior and basic drives related to physical exercise (Fuster, 2001) may be dependent of cardiovascular strain level.

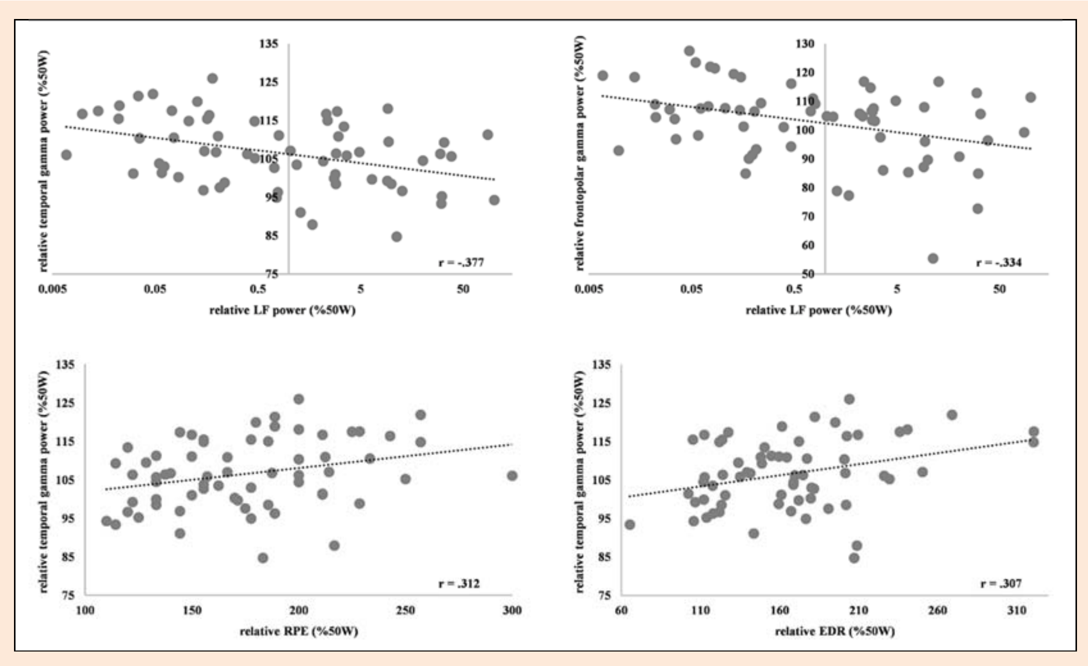

Figure 3. Correlations of temporal and frontopolar gamma power with LF power, EDR and RPE during GXT. GXT data normalized to 50W-values and presented as %50W, data of 50W excluded. LF and HF power plots with log-10 scale, r Spearman's rank correlation coefficient.

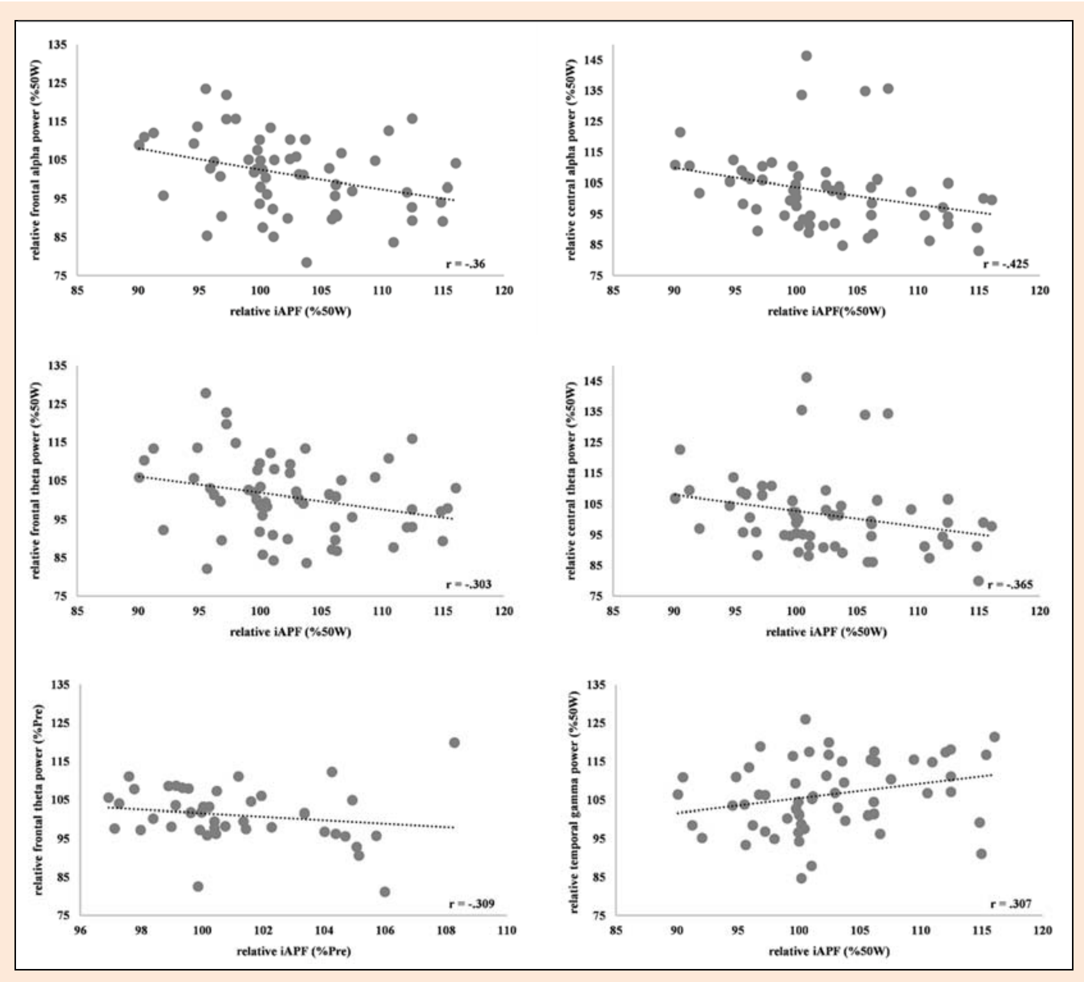

Figure 4. Correlations of specific EEG frequency band power with iAPF during GXT and in recovery. GXT data normalized to 50W-values and presented as %50W, data of 50W excluded. Post5-15 data normalized to Pre-values and presented as %Pre. r Spearman's rank correlation coefficient.

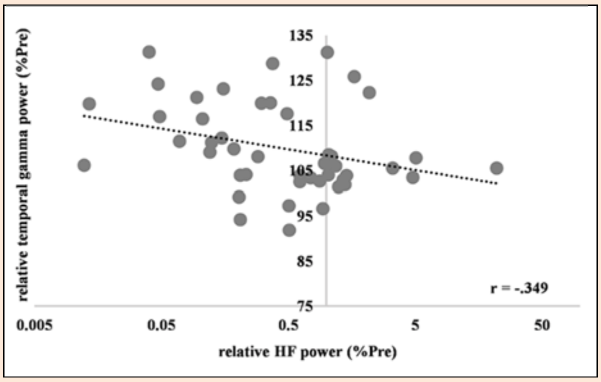

Figure 5. Correlation of temporal gamma power with HF power during recovery. Post5-15 data normalized to Pre-values and presented as %Pre. r Spearman's rank correlation coefficient.

Referring to the temporal lobe, the correlations may be in line with the assumptions already determined by pre- and acute post-exercise comparison. Evidence exists for a negative interaction of HRV frequency parameters with multisensory and sensorimotor integration (Jensen et al., 2007), working memory (Chang et al., 2013; Tsujii et al., 2013; Voss et al., 2020) and emotional processes (Robertson and Marino, 2016; Sakaki et al., 2016). Concerning the highest correlation of the temporal gamma power with RPE and the certain connection of the posterior cingulate cortex to the temporal lobe, the assumed functionality of the posterior cingulate cortex as a responsible structure for assessing perceived exertion could be supported (Fontes et al., 2015). The moderate correlation of EDR and temporal gamma power supports the existing relation of gamma activity (Herrero et al., 2018) and temporal lobe functions (Zelano et al., 2016) with changes in the respiratory rate. Referring to the occipital lobe with similar correlation effects to HRV, a provoked multisensory demand may be indicated including additional stress in visual processing. Visual processing appears to raise with increasing exercise intensity, though no specific, differing visual stimuli was given in GXT progression. However, this effect could be related to the instruction to focus on a picture on the wall during the GXT. Due to increasing exercise intensity, enhanced body movement is provoked which probably makes it more difficult to focus on the picture and minimize head movements. Therefore, interpretation of occipital effects due to pure cardiovascular strain has to be taken with caution. The highest negative correlation of HF power with the occipital lobe and temporal lobe, next to total power, may be interpreted that provoked multisensory processing is linked to reduced parasympathetic activity in context with an exhausting exercise. Summarizing the results and the interpretation of temporal and frontopolar correlations with HRV frequency domain, an increased connectedness of these lobes during physical exercise may be speculated. Considering the occipital lobe, further research of a potential influence of the visual stimulus during a GXT has to be conducted. Related to iAPF, no moderate correlations to HRV and RPE could be identified. Only in context with brain activity, a moderately negative correlation with EEG theta and alpha total power, even more particularly in the frontal and central lobe, and a moderately positive correlation with temporal gamma power could be found. These relations can be explained as followed: Increased iAPF is associated with increased allocation of attentional resources and somatosensory input (Mierau et al., 2017) as well as interpreted with higher information processing (Klimesch et al., 1996). Referring to frontal and central theta power, frontal midline theta power, as an indicator of top-down sustained attention is understood to be lower in context with optimal attentional engagement and higher with excessive attentional control (Kao et al., 2013). According to the negative correlation of theta power and iAPF, we hypothesize that during a GXT the psychophysiological effects related to an iAPF increase occur by means of a more efficient application of attentional resources. Furthermore, alpha power seems to play an important role in top-down anticipatory attention such that reduced alpha power indicate enhanced cortical excitability in task relevant areas (ElShafei et al., 2020), e.g. the frontal and central lobe in context of a GXT. The positive link of iAPF to temporal gamma power could be explained due to the fact that enhanced temporal gamma activity could be interpreted as provoked multisensory processing and attention (Jensen et al., 2007).

In the recovery process, solely temporal power of beta and gamma frequency as well as the total spectrum in EEG showed moderate negative correlations with HF power of HRV. EDR only revealed a small positive correlation to the temporal cortex supposing the respiratory rate to be less related to the temporal lobe at rest than during exercise. These aspects taken together, the relation of HF power to the temporal cortex can be interpreted as a prolonged negative relation of multisensory and sensorimotor integration, working memory and emotional processes to parasympathetic activity independent of the actual body activity carried out. During short- and middle-term recovery of an exhausting exercise, changes in the ANS are still expected due to a study determining effects one hour after a cycling exercise (Spring et al., 2018). Also, iAPF showed less moderate correlations in recovery than during the GXT. Only frontal theta correlated moderately negative with iAPF. This difference to GXT related correlations could rely on the relaxed recovery without the necessity of higher level of anticipatory attention and cortical excitability in task relevant brain areas (regarding alpha power reduction) as well as multisensory processing (regarding temporal gamma power increase). The inverse relation of theta power and iAPF could indicate a prolonged, more efficient use of attentional resources also during recovery after physical exhaustion. Summarizing, the hypothesis of a general negative relationship of EEG total spectrum power to HRV frequency parameters and a general positive relationship of EEG total spectrum power to RPE cannot be verified. According to different brain lobes and HRV relations between GXT conduction and rest, the hypothesized dependency of total brain activity on peripheral physiology should be reconsidered. It is recommended to differentiate between brain lobes regarding the particular provoked frontopolar and temporal lobe in this study. Although the correlation effects were just of a moderate to slightly strong level, they give sufficient information to foster a more precise investigation of the relationship between brain activity and HRV.

Conclusion

Overall, this study corroborates the existence of a (neuro-) physiological and subjectively perceived strain and their interaction evoked by pure, exhaustive physical activity. To our knowledge, the revealed effects in the temporal lobe may be declared as novel findings, as such that the temporal lobe also seems to play an important role in the interaction of brain activity and the cardiovascular system, next to the PFC. Furthermore, according to the original interpretation of Fisher's statistics our results provide enough basis to be encouraged to conduct further similar studies. An analysis of brain lobe connectivity or a windowed Fourier analysis to compare time-dependent alterations in context with HRV presents further interesting research intentions. Based on the results of this study, we strongly recommend considering possible effects of pure physical activity in studies with an additional research question.

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References

Abeln, V., Schneider, S., Knicker, A., Schiffer, T., Hollmann, W. and 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),** 105-116.

Abhang, P. A., Gawali, B. W. and Mehrotra, S. C. (2016) Technical aspects of brain rhythms and speech parameters *Introduction to EEG- and Speech-Based Emotion Recognition* . Elsevier. 51-79.

Aftanas, L. I. and Golocheikine, S. A. (2001) Human anterior and frontal midline theta and lower alpha reflect emotionally positive state and internalized attention: high-resolution EEG investigation of meditation. *Neuroscience Letters* **310(1)**, 57-60.

Ako, M., Kawara, T., Uchida, S., Miyazaki, S., Nishihara, K., Mukai, J., Hirao, J., Ako, J. and Okubo, Y. (2003) Correlation between electroencephalography and heart rate variability during sleep. *Psychiatry and Clinical Neuroscience* **57(1)**, 59-65.

Baddeley, A. (2000) The episodic buffer: a new component of working memory? *Trends in Cognitive Sciences* **4(11)**, 417-423.

Bailey, S. P., Hall, E. E., Folger, S. E. and Miller, P. C. (2008) Changes in EEG during graded exercise on a recumbent cycle ergometer. *Journal of Sports Science and Medicine* **7(4)**, 505–511.

Banach, T., Grandys, M., Juszczak, K., Kolasińska-Kloch, W., Zoładź, J., Laskiewicz, J. and Thor, P. J. (2004) Heart rate variability during incremental cycling exercise in healthy untrained young men. *Folia medica Cracoviensia* **45(1-2)**, 3-12.

Bertollo, M., Doppelmayr, M. and Robazza, C. (2019) Using brain technology in practice. In: *Handbook of Sport Psychology.* Eds: G. Tenenbaum and R. Eklund. 4th edition. Hoboken: Wiley & Blackwell.

Borg, G. a. V. (1982). Psychophysical bases of perceived exertion. *Medicine and Science in Sports and Exercise* **14(5)**, 377.

Brümmer, V., Schneider, S., Strüder, H. K. and Askew, C. D. (2011) Primary motor cortex activity is elevated with incremental exercise intensity. *Neuroscience* **181**, 150–162.

Buchheit, M., Laursen, P. B. and Ahmaidi, S. (2007) Parasympathetic reactivation after repeated sprint exercise. *American Journal of Physiology - Heart and Circulatory Physiology* **293(1)**, H133-141.

Candido, N., Okuno, N. M., da Silva, C. C., Machado, F. A. and Nakamura, F. Y. (2015) Reliability of the heart rate variability threshold using visual inspection and dmax methods. *International Journal of Sports Medicine* **36(13)**, 1076–1080

Cavanagh, J. F. and Frank, M. J. (2014). Frontal theta as a mechanism for cognitive control. *Trends in Cognitive Sciences* **18(8)**, 414-421.

Chang, Y. K., Huang, C. J., Chen, K. F. and Hung, T. M. (2013) Physical activity and working memory in healthy older adults: an ERP study. *Psychophysiology* **50(11)**, 1174-1182.

Chang, Y. K., Labban, J. D., Gapin, J. I. and Etnier, J. L. (2012) The effects of acute exercise on cognitive performance: A meta-analysis. *Brain Research* **1453**, 87–101.

Cheron, G., Petit, G., Cheron, J., Leroy, A., Cebolla, A., Cevallos, C., Petieau, M., Hoellinger, T., Zarka, D., Clarinval, A. and Dan, B. (2016) Brain oscillations in sport: Toward EEG biomarkers of performance. *Frontiers in Psychology* **7**, 246.

Cohen, J. (1988) *Statistical power analysis for the behavioral sciences.* 2nd edition. New York: Routledge.

Cohen, J. (1992). Statistical power analysis. *Current Directions in Psychological Science* **1(3)**, 98-101.

Corcoran, A. W., Alday, P. M., Schlesewsky, M. and Bornkessel-Schlesewsky, I. (2018) Toward a reliable, automated method of individual alpha frequency (IAF) quantification. *Psychophysiology* **55(7)**, e13064.

Cox, E. P., O'Dwyer, N., Cook, R., Vetter, M., Cheng, H. L., Rooney, K. and O'Connor, H. (2016) Relationship between physical activity and cognitive function in apparently healthy young to middle-aged adults: A systematic review. *Journal of Science and Medicine in Sport* **19(8)**, 616–628.

Crabbe, J. B. and Dishman, R. K. (2004) Brain electrocortical activity during and after exercise: A quantitative synthesis. *Psychophysiology* **41(4)**, 563–574.

Cruz, C. J. G., Rolim, P.S., Pires, D. S., Mendes, C. M. O., Paula, G. M. , Porto, L. G. G., Garcia, G. L. and Molina, G. E. (2017) Reliability of heart rate variability threshold and parasympathetic reactivation after a submaximal exercise test. *Motriz: Revista de Educação Física* **23(1)**, 65–70.

Cuffaro, M. (2011) Fine motor skills. In; *Encyclopedia of child behavior and development*. Eds: S. Goldstein and J. A. Naglieri. Boston, MA: Springer US. 657-657.

Cysarz, D., Zerm, R., Bettermann, H., Fruhwirth, M., Moser, M. and Kroz, M. (2008) Comparison of respiratory rates derived from heart rate variability, ECG amplitude, and nasal/oral airflow. *Annals of Biomedical Engineering* **36(12)**, 2085-2094.

da Silva, W. Q. A., Fontes, E. B., Forti, R. M., Lima, Z. L., Machado, D., Deslandes, A. C., Hussey, E., Ward, N., Mesquita, R. C., Okano, A. H. and Elsangedy, H. M. (2017) Affect during incremental exercise: The role of inhibitory cognition, autonomic cardiac function, and cerebral oxygenation. *PLoS One* **12(11)**, e0186926.

Davranche, K., Brisswalter, J. and Radel, R. (2015) Where are the limits of the effects of exercise intensity on cognitive control? *Journal of Sport and Health Science* **4(1)**, 56-63.

di Fronso, S., Aquino, A., Bondár, R. Z., Montesano, C., Robazza, C. and Bertollo, M. (2020) The influence of core affect on cyclo-ergometer endurance performance: Effects on performance outcomes and perceived exertion. *Journal of Sport and Health Science*. In Press.

di Fronso, S., Fiedler, P., Tamburro, G., Haueisen, J., Bertollo, M. and Comani, S. (2019) Dry EEG in sports sciences: A fast and reliable tool to assess individual alpha peak frequency changes induced by physical effort. *Frontiers in Neuroscience* **13**, 982.

di Fronso, S., Robazza, C., Bortoli, L. and Bertollo, M. (2017) Performance optimization in sport: A psychophysiological approach. *Motriz: Revista de Educação Física* **23(4)**. E-Pub, Nov 27.

Dickhuth, H.-H. and Badtke, G. (2010) *Sportmedizin für Ärzte: Lehrbuch auf der Grundlage des Weiterbildungssystems der Deutschen Gesellschaft für Sportmedizin und Prävention (DGSP)* (2., überarb. Aufl. ed.). Köln: Dt. Ärzte-Verl.

Duarte, T. S., Ferreira Júnior, A. J., Rezende, E. C., Pertence, L. C., Marins, J. C. B. and Lima, J. R. P. (2014) Association between heart rate variability threshold and post-exercise vagal reactivation. *JEPonline* **17(5)**, 58–64.

Dykstra, R. M., Hanson, N. J. and Miller, M. G. (2019). Brain activity during self-paced vs. fixed protocols in graded exercise testing. *Exp Brain Res*. doi: 10.1007/s00221-019-05669-x.

Edwards, A. M., Deakin, G. B. and Guy, J. H. (2016). Brain and cardiorespiratory responses to exercise in hot and thermoneutral conditions. *International Journal of Sports Medicine* **37(10)**, 779–784.

Ehrhart, J., Toussaint, M., Simon, C., Gronfier, C., Luthringer, R. and Brandenberger, G. (2000). Alpha activity and cardiac correlates: three types of relationships during nocturnal sleep. *Clinical Neurophysiology* **111(5)**, 940-946.

ElShafei, H. A., Fornoni, L., Masson, R., Bertrand, O. and Bidet-Caulet, A. (2020) Age-related modulations of alpha and gamma brain activities underlying anticipation and distraction. *PLoS One* **15(3)**, e0229334.

Esposito, G. and Vivanti, G. (2013) Gross motor skills. In: *Encyclopedia of autism spectrum disorders*. Ed: F. R. Volkmar. New York, NY: Springer. 1459-1462.

Etnier, J. L. and Chang, Y. K. (2019) Exercise, cognitive function, and the brain: Advancing our understanding of complex relationships. *Journal of Sport and Health Science* **8(4)**, 299-300.

Etnier, J. L., Salazar, W., Landers, D. M., Petruzzello, S. J., Han, M. and Nowell, P. (1997) The influence of physical fitness and exercise upon cognitive functioning: A meta-analysis. *Journal of Sport and Exercise Psychology* **19(3)**, 249–277.

Faulkner, J. and Eston, R. (2007) Overall and peripheral ratings of perceived exertion during a graded exercise test to volitional exhaustion in individuals of high and low fitness. *European Journal of Applied Physiology* **101(5)**, 613-620.

Fontes, E. B., Okano, A. H., Guio, F., Schabort, E. J., Min, L. L., Basset, F. A., Stein, D. J. and Noakes, T. D. (2015) Brain activity and perceived exertion during cycling exercise: An fMRI study. *British Journal of Sports Medicine* **49(8)**, 556–560.

Furley, P. and Wood, G. (2016) Working memory, attentional control, and expertise in sports: a review of current literature and directions for future research. *Journal of Applied Research in Memory and Cognition* **5(4)**, 415-425.

Fuster, J. n. M. (2001) The prefrontal cortex - An update. *Neuron* **30(2)**, 319–333.

Garcia, A., Uribe, C. E., Tavares, M. C. and Tomaz, C. (2011) EEG and autonomic responses during performance of matching and non-matching to sample working memory tasks with emotional content. *Frontiers in Behavioral Neuroscience* **5**, 82.

Gigerenzer, G. (2004) Mindless statistics. *The Journal of Socio-Economics* **33(5)**, 587-606.

Gutmann, B., Mierau, A., Hulsdunker, T., Hildebrand, C., Przyklenk, A., Hollmann, W. and Struder, H. K. (2015) Effects of physical exercise on individual resting state EEG alpha peak frequency. *Neural Plast* **2015**, 717312.

Gutmann, B., Zimmer, P., Hulsdunker, T., Lefebvre, J., Binnebossel, S., Oberste, M., and Mierau, A. (2018) The effects of exercise intensity and post-exercise recovery time on cortical activation as revealed by EEG alpha peak frequency. *Neuroscience Letters* **668**, 159-163.

Herrero, J. L., Khuvis, S., Yeagle, E., Cerf, M. and Mehta, A. D. (2018) Breathing above the brain stem: volitional control and attentional modulation in humans. *Journal of Neurophysiology* **119(1)**, 145-159.

Herrmann, C. S., Fründ, I. and Lenz, D. (2010) Human gamma-band activity: A review on cognitive and behavioral correlates and network models. *Neuroscience and Biobehavioral Reviews* **34(7)**, 981–992.

Huonker, M. (2004) Freizeit- und Fitnesssport: Präventiver Gesundheits-/Fitness-Check [Leisure and fitness sports: Preventive health/fitness check]. *Sportorthopädie - Sporttraumalogie* **20(2)**, 65–69.

Impellizzeri, F. M., Marcora, S. M. and Coutts, A. J. (2019) Internal and External Training Load: 15 Years On. *International Journal of Sports Physiology and Performance* **14(2)**, 270-273.

Impellizzeri, F. M., Rampinini, E., Coutts, A. J., Sassi, A. and Marcora, S. M. (2004) Use of RPE-based training load in soccer. *Medicine & Science in Sports & Exercise* **36(6)**, 1042-1047.

Jann, K., Koenig, T., Dierks, T., Boesch, C. and Federspiel, A. (2010) Association of individual resting state EEG alpha frequency and cerebral blood flow. *Neuroimage* **51(1)**, 365-372.

Jensen, O., Kaiser, J. and Lachaux, J.-P. (2007) Human gamma-frequency oscillations associated with attention and memory. *Trends in Neurosciences* **30(7)**, 317–324.

Jung, R., Moser, M., Baucsek, S., Dern, S. and Schneider, S. (2015) Activation patterns of different brain areas during incremental exercise measured by near-infrared spectroscopy. *Experimental brain research* **233(4)**, 1175–1180.

Kaikkonen, P., Rusko, H. and Martinmaki, K. (2008) Post-exercise heart rate variability of endurance athletes after different high-intensity exercise interventions. *Scandinavian Journal of Medicine & Science in Sports* **18(4)**, 511-519.

Kao, S. C., Huang, C. J. and Hung, T. M. (2013) Frontal midline theta is a specific indicator of optimal attentional engagement during skilled putting performance. *Journal of Sport and Exercise Psychology* **35(5)**, 470-478.

Kayser, B. (2003). Exercise starts and ends in the brain. *European Journal of Applied Physiology* **90(3-4)**, 411-419.

Kleiger, R. E., Stein, P. K. and Bigger, J. T. (2005) Heart rate variability: Measurement and clinical utility. *Annals of Noninvasive Electrocardiology: the official journal of the International Society for Holter and Noninvasive Electrocardiology, Inc* **10(1)**, 88–101.

Klimesch, W., Doppelmayr, M., Schimke, H. and Pachinger, T. (1996) Alpha frequency, reaction time, and the speed of processing information. *Journal of Clinical Neurophysiology* **13(6)**, 511-518.

Kolb, B. and Whishaw, I. Q. (2009) *Fundamentals of human neuropsychology*. 6. edition. 4. printing ed. New York: Worth Publ.

Kraaier, V., van Huffelen, A. C. and Wieneke, G. H. (1988) Changes in quantitative EEG and blood flow velocity due to standardized hyperventilation; a model of transient ischaemia in young human subjects. *Electroencephalography and Clinical Neurophysiology* **70(5)**, 377–387.

Kraaier, V., van Huffelen, A. C., Wieneke, G. H., van der Worp, H. B. and Bär, P. R. (1992). Quantitative EEG changes due to cerebral vasoconstriction. Indomethacin versus hyperventilation-induced reduction in cerebral blood flow in normal subjects. *Electroencephalography and Clinical Neurophysiology* **82(3)**, 208–212.

Kuo, T. B., Chen, C. Y., Hsu, Y. C. and Yang, C. C. (2016) EEG beta power and heart rate variability describe the association between cortical and autonomic arousals across sleep. *Autonomic Neuroscience: Basic & Clinical* **194**, 32-37.

Kuo, T. B., Lin, T., Yang, C. C., Li, C. L., Chen, C. F. and Chou, P. (1999) Effect of aging on gender differences in neural control of heart rate. *The American Journal of Physiology* **277(6)**, H2233-2239.

Lambourne, K. and Tomporowski, P. (2010) The effect of exercise-induced arousal on cognitive task performance: a meta-regression analysis. *Brain Research* **1341**, 12-24.

Lohse, K. R. and Sherwood, D. E. (2011). Defining the focus of attention: effects of attention on perceived exertion and fatigue. *Frontiers in Psychology* **2**, 332.

Maceri, R. M. and Cherup, N. P. H., N. J. (2019) EEG responses to incremental self-paced cycling exercise in young and middle aged adults. *International Journal of Exercise Science* **12(3)**, 800-810.

Makeig, S., Bell, A., Jung, T. and Sejnowski, T. (1996) Independent component analysis of electroencephalographic data. *Advances in Neural Information Processing Systems* **8**, 145–151.

Malik, A. S. and Amin, H. U. (2017) *Designing EEG experiments for studying the brain: Design code and example datasets*. Oxford: Elsevier.

McMorris, T., Hale, B. J., Corbett, J., Robertson, K. and Hodgson, C. I. (2015). Does acute exercise affect the performance of whole-body, psychomotor skills in an inverted-U fashion? A meta-analytic investigation. *Physiology & Behavior* **141**, 180-189.

Mechau, D., Mücke, S., Weiss, M. and Liesen, H. (1998) Effect of increasing running velocity on electroencephalogram in a field test. *European Journal of Applied Physiology and Occupational Physiology* **78(4)**, 340–345.

Michael, S., Graham, K. S. and Davis, G. M. (2017) Cardiac autonomic responses during exercise and post-exercise recovery using heart

rate variability and systolic time intervals - A review. *Frontiers in Physiology* **8**, 301.
Michel, C. M. and Brunet, D. (2019) EEG Source Imaging: A Practical Review of the Analysis Steps. [Review]. *Front Neurol* **10**, 325.
Mierau, A., Klimesch, W. and Lefebvre, J. (2017) State-dependent alpha peak frequency shifts: Experimental evidence, potential mechanisms and functional implications. *Neuroscience* **360**, 146-154.
Moraes, H., Ferreira, C., Deslandes, A., Cagy, M., Pompeu, F., Ribeiro, P. and Piedade, R. (2007) Beta and alpha electroencephalographic activity changes after acute exercise. *Arquivos de Neuro-Psiquiatria* **65(3a)**, 637–641.
Neyman, J. and Pearson, E. S. (1933). On the problem of the most efficient tests of statistical hypotheses. *Philosophical transactions of the royal society of London* **231**, 289-337.
Nielsen, B. and Nybo, L. (2003) Cerebral changes during exercise in the heat. *Sports Medicine (Auckland, N.Z.)* **33(1)**, 1–11.
Nuzzo, R. (2014) Scientific method: Statistical errors. *Nature* **506(7487)**, 150-152.
Park, J. L., Fairweather, M. M. and Donaldson, D. I. (2015) Making the case for mobile cognition: EEG and sports performance. *Neuroscience & Biobehavioral Reviews* **52**, 117-130.
Ray, W. J. and Cole, H. W. (1985) EEG alpha activity reflects attentional demands, and beta activity reflects emotional and cognitive processes. *Science (New York, N.Y.)* **228(4700)**, 750–752.
Robertson, C. V. and Marino, F. E. (2015) Prefrontal and motor cortex EEG responses and their relationship to ventilatory thresholds during exhaustive incremental exercise. *European Journal of Applied Physiology* **115(9)**, 1939–1948.
Robertson, C. V. and Marino, F. E. (2016) A role for the prefrontal cortex in exercise tolerance and termination. *Journal of Applied Physiology* **120(4)**, 464-466.
Sakaki, M., Yoo, H. J., Nga, L., Lee, T. H., Thayer, J. F. and Mather, M. (2016) Heart rate variability is associated with amygdala functional connectivity with MPFC across younger and older adults. *Neuroimage* **139**, 44-52.
Schneider, S., Rouffet, D. M., Billaut, F. and Strüder, H. K. (2013) Cortical current density oscillations in the motor cortex are correlated with muscular activity during pedaling exercise. *Neuroscience* **228**, 309–314.
Serrien, D. J., Ivry, R. B. and Swinnen, S. P. (2006) Dynamics of hemispheric specialization and integration in the context of motor control. *Nature reviews. Neuroscience* **7(2)**, 160–166.
Shaffer, F. and Ginsberg, J. P. (2017) An overview of heart rate variability metrics and norms. *Frontiers in Public Health* **5**, 258.
Shiraishi, Y., Katsumata, Y., Sadahiro, T., Azuma, K., Akita, K., Isobe, S., Yashima, F., Miyamoto, K., Nishiyama, T., Tamura, Y., Kimura, T., Nishiyama, N., Aizawa, Y., Fukuda, K. and Takatsuki, S. (2018) Real-time analysis of the heart rate variability during incremental exercise for the detection of the ventilatory threshold. *Journal of the American Heart Association* **7(1)**. January 2018, Epub.
Spring, J. N., Bourdillon, N. and Barral, J. (2018) Resting EEG microstates and autonomic heart rate variability do not return to baseline one hour after a submaximal exercise. *Front Neurosci* **12**, 460.
St Clair Gibson, A., Lambert, E. V., Rauch, L. H., Tucker, R., Baden, D. A., Foster, C. and Noakes, T. D. (2006) The role of information processing between the brain and peripheral physiological systems in pacing and perception of effort. *Sports Medicine* **36(8)**, 705-722.
Stegmüller, W. (1973) Personelle und statistische Wahrscheinlichkeit [Personal and statistical probability] *Probleme und Resultate der Wissenschaftstheorie und analytischen Philosophie [Problems and results of philosophy of science and analytical philosophy]*. Berlin, Heidelberg, New York: Springer.
Stein, A. and Sarnthein, J. (2000) Different frequencies for different scales of cortical integration: From local gamma to long range alpha/theta synchronization. *International Journal of Psychophysiology* **38(3)**, 301–313.
Sun, T. and Walsh, C. A. (2006) Molecular approaches to brain asymmetry and handedness. *Nature reviews. Neuroscience* **7(8)**, 655–662.
Sun, X., Li, Y., Cai, L. and Wang, Y. (2020) Effects of physical activity interventions on cognitive performance of overweight or obese children and adolescents: a systematic review and meta-analysis. *Pediatric Research*. Online ahead of print.
Tang, Y. Y., Ma, Y., Fan, Y., Feng, H., Wang, J., Feng, S., Lu, Q., Hu, B., Lin, Y., Li, J., Zhang, Y., Wang, Y., Zhou, L. and Fan, M. (2009) Central and autonomic nervous system interaction is altered by short-term meditation. *Proceedings of the National Academy of Sciences U S A* **106(22)**, 8865-8870.
Tarvainen, M. P., Ranta-Aho, P. O. and Karjalainen, P. A. (2002). An advanced detrending method with application to HRV analysis. *IEEE Transactions on Bio-Medical Engineering* **49(2)**, 172–175.
Tomporowski, P. D. (2003). Effects of acute bouts of exercise on cognition. *Acta Psychol (Amst)* **112(3)**, 297-324.
Triggiani, A. I., Valenzano, A., Del Percio, C., Marzano, N., Soricelli, A., Petito, A., Bellomo, A., Basar, E., Mundi, C., Cibelli, G. and Babiloni, C. (2016). Resting state Rolandic mu rhythms are related to activity of sympathetic component of autonomic nervous system in healthy humans. *International Journal of Psychophysiology: official journal of the International Organization of Psychophysiology* **103**, 79–87.
Tsujii, T., Komatsu, K. and Sakatani, K. (2013) Acute effects of physical exercise on prefrontal cortex activity in older adults: a functional near-infrared spectroscopy study. *Advances in Experimental Medicine and Biology* **765**, 293-298.
Umetani, K., Singer, D. H., McCraty, R. and Atkinson, M. (1998) Twenty-four hour time domain heart rate variability and heart rate: Relations to age and gender over nine decades. *Journal of the American College of Cardiology* **31(3)**, 593–601.
Voss, M. W., Weng, T. B., Narayana-Kumanan, K., Cole, R. C., Wharff, C., Reist, L., DuBose, L., Sigurdsson, G., Mills, J. A., Long, J. D., Magnotta, V. A. and Pierce, G. L. (2020) Acute exercise effects predict training change in cognition and connectivity. *Medicine & Science in Sports and Exercise*. **52(1),** 131-140.
Wackermann, J. and Matousek, M. (1998) From the 'EEG age' to a rational scale of brain electric maturation. *Electroencephalography and Clinical Neurophysiology* **107(6)**, 415–421.
Wada, Y., Takizawa, Y., Jiang, Z. Y. and Yamaguchi, N. (1994) Gender differences in quantitative EEG at rest and during photic stimulation in normal young adults. *Clinical EEG (electroencephalography)* **25(2)**, 81–85.
Whitley, E. and Ball, J. (2002) Statistics review 6: Nonparametric methods. *Critical Care* **6(6)**, 509-513..
Yamamoto, Y., Hughson, R. L. and Nakamura, Y. (1992) Autonomic nervous system responses to exercise in relation to ventilatory threshold. *Chest* **101(5 Suppl)**, 206S–210S.
Zelano, C., Jiang, H., Zhou, G., Arora, N., Schuele, S., Rosenow, J. and Gottfried, J. A. (2016) Nasal respiration entrains human limbic oscillations and modulates cognitive function. *Journal of Neuroscience* **36(49)**, 12448-12467.
Zschocke, S. and Hansen, H. (2012) *Klinische Elektroenzephalographie [Clinical electroencephalography]*. Berlin, Heidelberg: Springer.

Key points

- Temporal lobe EEG activity is persistently increased due to GXT.
- Frontopolar and temporal lobe EEG activity correlates moderately negative with HRV frequency parameters during GXT.
- Temporal lobe gamma activity correlates moderately positive with RPE.
- Temporal lobe EEG activity correlates moderately negative with HF power in recovery.

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