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Inverted U-shape-like functional connectivity alterations in cognitive resting-state networks depending on exercise intensity: An fMRI study

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ABSTRACT

Acute physical activity influences cognitive performance. However, the relationship between exercise intensity, neural network activity, and cognitive performance remains poorly understood. This study examined the effects of different exercise intensities on resting-state functional connectivity (rsFC) and cognitive performance. Twenty male athletes (27.3 ± 3.6 years) underwent cycling exercises of different intensities (high, low, rest/control) on different days in randomized order. Before and after, subjects performed resting-state functional magnetic resonance imaging and a behavioral Attention Network Test (ANT). Independent component analysis and Linear mixed effects models examined rsFC changes within ten resting-state networks. No significant changes were identified in ANT performance. Resting-state analyses revealed a significant interaction in the Left Frontoparietal Network, driven by a non-significant rsFC increase after low-intensity and a significant rsFC decrease after high-intensity exercise, suggestive of an inverted U-shape relationship between exercise intensity and rsFC. Similar but trend-level rsFC interactions were observed in the Dorsal Attention Network (DAN) and the Cerebellar Basal Ganglia Network. Explorative correlation analysis revealed a significant positive association between rsFC increases in the right superior parietal lobule (part of DAN) and better ANT orienting in the low-intensity condition. Results indicate exercise intensity-dependent subacute rsFC changes in cognition-related networks, but their cognitive-behavioral relevance needs further investigation.

1. Introduction

There is a general consensus in the literature that acute physical exercise exerts important influences on cognitive performance, with suggestions for positive influences in particular for light- to moderate-intensity (aerobic) exercise (Basso & Suzuki, 2017; Chang et al., 2012; Ishihara et al., 2021; Lambourne & Tomporowski, 2010). While early research mainly assessed basic aspects of sensory and motor cognition or information processing speed, there is a recent shift to complex forms of cognition, especially executive functions (EF) (Pontifex et al., 2019). On

Abbreviations: ANT, Attention Network Test; BOLD, Blood oxygenation level-dependent; CB, Cerebellum; CBN, Cerebellar Basal Ganglia Network; DAN, Dorsal Attention Network; EF, Executive Functions; fMRI, Functional magnetic resonance imaging; HIIE, High-Intensity Interval Exercise; HR, Heart rate; HR_{int}, Heart rate during exercise intervention; HR_{rest}, Heart rate during resting-state functional MRI; ICA, Independent component analysis; LFPN, Left Frontoparietal Network; LIIE, Low-Intensity Interval Exercise; LME, Linear mixed effects model; MRI, Magnetic resonance imaging; RFPN, Right Frontoparietal Network; RPE, Rating of perceived exertion; rsFC, resting-state Functional Connectivity; rs-fMRI, Resting-state fMRI; RSN, Resting-state network; RT, Reaction Time (ms); SFG, Superior frontal gyrus; SPL, Superior parietal lobule; VO_{2max}, Maximal oxygen uptake (mL/min/kg).

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the other hand, the literature examining the effects of acute high-intensity (anaerobic) exercise bouts on cognitive performance is relatively small, with more variable results: Beyond some evidence for detrimental effects on complex cognitive functions (especially EF) *during* high-intensity exercise, there are also studies suggesting positive *after-effects* of high-intensity continuous and also interval exercise (Hsieh et al., 2021; Moreau & Chou, 2019; Sudo et al., 2022). Especially the latter form of training has gained interest due to its presumed time efficiency, which may help overcome motivational barriers to engage in regular physical exercise (Hsieh et al., 2021).

Various methodological and physiological factors, e.g., exercise mode, intensity and duration, timing and type of cognitive task, or physical fitness of participants, may moderate the situation-specific influence of the exercise-induced physiological brain changes during and immediately after exercise on observable cognitive changes (Pontifex et al., 2019; Sudo et al., 2022). In fact, these physiological mechanisms remain poorly understood. Some researchers have speculated on such mechanisms to explain inverted U-shaped relationships between exercise intensity and cognitive performance (Davey, 1973; Gutin, 1973), according to Yerkes and Dodson's law (Yerkes & Dodson, 1908): Observations of cognitive improvement at moderate exercise intensity are assumed to be induced by an optimal level of activity ("arousal"), while performance at light and very high training intensities suffers from relative under- or overactivation. However, the mechanistic basis of these arousal changes is underspecified (Pontifex et al., 2019): For example, an exercise-induced increase in brain catecholamines (especially noradrenaline and dopamine) is frequently discussed as the physiological underpinning, whereby a moderate increase in catecholamines exerts a positive influence on cognitive performance by improving the signal-to-noise ratio, however, low neuromodulation by light exercise, and an excessive increase in catecholamines by high-intensity exercise seem to weaken the signal-to-noise ratio and to impair cognitive performance ("catecholamine hypothesis") (Arnsten, 2011; Cooper, 1973; McMorris et al., 2016; Sudo et al., 2022). This converges with more recent models discussing a modulatory role of the noradrenergic locus coeruleus (Pontifex et al., 2019). Nevertheless, previous studies on the inverted-U theory and the underlying neurochemical mechanisms are inconsistent (Basso & Suzuki, 2017; Chang et al., 2012; Lambourne & Tomporowski, 2010; McMorris et al., 2015; Moreau & Chou, 2019; Sudo et al., 2022), so this issue requires further empirical confirmation and a deeper understanding of the underlying brain mechanisms. Moreover, exercise-induced increases in cerebral blood flow and cerebral oxygenation could facilitate cognitive functioning by improving metabolic resources, but this may mainly apply for moderate-intensity to vigorous exercise and not for very high-intensity levels (Rooks et al., 2010). The transient hypofrontality model even proposes that metabolic supply for prefrontal areas is reduced in favor of adjacent motor-related areas during very high workloads (Dietrich & Audiffren, 2011). Again, empirical evidence is limited, and the physiological effects do not seem to sustain long enough after exercise termination to satisfactorily explain cognitive after-effects (Pontifex et al., 2019; Sudo et al., 2022).

From the abovementioned frameworks, it can be predicted that these modulatory changes should exert downstream effects on the functioning of large-scale brain networks, i.e., induce similar (curvi)linear relationships between interregional functional connectivity patterns and exercise intensity as on the behavioral level: Resting-state functional connectivity (rsFC), as opposed to structural connectivity via anatomical connections, is described as interactions between anatomically separate brain regions with correlating neuronal activation patterns (Eickhoff & Müller, 2015; Friston, 1994; van den Heuvel & Hulshoff Pol, 2010). Neuronal activity can be measured using BOLD (blood oxygenation level-dependent) signal changes (Ogawa et al., 1990). Based on statistical similarities in their BOLD signal over time during rest, brain regions can be grouped into resting-state networks (RSNs) (Biswal et al., 1995; Damoiseaux et al., 2006). Experimental studies with functional magnetic resonance imaging (fMRI), as one essential method measuring rsFC, promise to be informative as they allow the parallel measurement of changes in rsFC in different cognitive networks as a function of exercise intensity, in combination with cognitive task performance. Up to now, however, only very few fMRI studies have examined the impact of acute physical exercise on rsFC in RSNs (Ko et al., 2023; Rajab et al., 2014; Schmitt et al., 2019; Weng et al., 2017) as also reviewed by Won et al. (2021). Using a within-subject design, one study examined the effect of aerobic exercise of moderate intensity on RSNs directly in comparison with a control condition (passive cycling; very light exercise intensity), testing for differences between younger and older healthy adults (Weng et al., 2017). Authors reported rsFC within, among others, the Executive Control Network (ECN; associated with attention and executive control) to increase after moderate-intensity exercise in both age groups, with moderate exercise having a higher impact on rsFC in the subgroup of older subjects (Weng et al., 2017). While the above-mentioned investigations solely focused on moderate-intensity exercise interventions, there is still very limited experimental evidence on the differential impact of low- to moderate versus high exercise intensities on RSNs within the same cohort. To the best of our knowledge, the only published study we are aware of examining the influence of aerobic and anaerobic exercise intensities on different RSNs in one cohort was from our group (Schmitt et al., 2019). Results revealed, among others, significant interaction effects in the Right Frontoparietal Network (FPN), where substantial changes in rsFC were driven by aerobic exercise. Interestingly, a recent study provided evidence for non-linear associations between exercise intensity and both cognitive performance in a visuospatial attention task and rsFC changes in the Dorsal Attention Network (DAN), consistent with an inverted U-shape function, but not in the Default Mode Network (DMN), which tended to show a linear relationship (Ko et al., 2023). Thus, modulation of rsFC by exercise intensity may vary depending on the specific RSN.

The small number and the heterogeneous nature of existing resting-state fMRI (rs-fMRI) studies with different study designs (between-group, within-group design examining one training intensity, within-group design examining two training intensities) indicate that there is as yet not enough empirical evidence to disentangle training intensity-dependent effects on cognitive RSNs in previous imaging research, including possible inverted U-shaped relationships between these two factors. Moreover, studies to date did not attempt to test the significance of modulatory changes in these rsFC networks for actual cognitive performance changes. Tasks measuring inhibitory aspects of EF provide a primary target here, as paradigms that tap into this functional domain (e.g., Flanker or Stroop interference resolution tasks) were frequently used in the behavioral and neurophysiological literature and indicated significant after-effects (Moreau & Chou, 2019; Pontifex et al., 2019), also after acute high-intensity exercise bouts (Hsieh et al., 2021). Meanwhile, acute effects of high-intensity exercise on RSN organization may also modulate lower, "bottom-up"-oriented aspects of cognitive functioning, like phasic alertness after the presentation of warning cues (Huertas et al., 2011; see also Chang et al., 2015), suggesting that it makes sense to investigate different levels of cognitive processing in parallel.

Hence, to extend the investigations on exercise intensity-dependent rsFC changes in RSNs, the current study examined healthy, young, and well-trained subjects (endurance athletes) using a within-subject cross-over study design that included a rest (control) condition, an aerobic (low-intensity), and an anaerobic (high-intensity) condition. Furthermore, a short version of the Attention Network Test (ANT), which examines 'alerting,' 'orienting,' and 'executive' aspects of attention in a common task framework (Posner & Rothbart, 2007), was studied to link changes in rsFC and cognitive/attentional behavior in the context of different exercise intensities. We hypothesized intensity-dependent cognitive behavioral and rsFC changes: i) improved cognitive performance in the ANT after the aerobic condition and decreased cognitive performance after the anaerobic condition; and ii) increased rsFC in cognitive RSNs after the aerobic intervention condition and decreased rsFC after the anaerobic intervention condition; and iii) rsFC changes in cognitive networks to correlate with improvements in cognitive performance.

2. Material and methods

2.1. Participants

Trained male cyclists aged 20–35 were recruited via flyer distribution at the local university, local cycling and triathlon clubs, and social media. Inclusion criteria were right-handedness, exercising at least five hours per week for the past three months, and relative maximum oxygen uptake (relVO$_{2max}$) of at least 55 ml/min/kg (De Pauw et al., 2013). Exclusion criteria were past or current psychiatric or neurological illnesses, cardiovascular or orthopedic diseases, head injuries, and MRI contraindications (i.e., non-removable metal, large tattoos, or claustrophobia).

All participants were informed about the study's intention, and written informed consent was obtained after a detailed explanation of all tests, potential discomforts, risks, and procedures employed in the investigation. The study was approved by the University Hospital Bonn Ethics Committee (no. 358/19) and was conducted according to national legislation and the Declaration of Helsinki.

2.2. Experimental procedures

2.2.1. General study design

'BEACON' (**B**icycling **E**ffects on **A**ffect and **CO**gnition in **N**euroscience) is a randomized exercise study investigating the neurobiological effects of acute physical activity of different intensities on mood and cognitive performance and their relation to corresponding neural networks. Behavioral and fMRI data at 3 T were acquired directly before and after three different experimental conditions on three days (Fig. 1).

At the beginning of the study, several questionnaires were used to characterize the sample: a socio-demographic questionnaire was acquired to collect characteristics such as age and education level; handedness was assessed using the Edinburgh Handedness Inventory (EHI) (Oldfield, 1971); verbal intelligence level was estimated by a German vocabulary test (Wortschaftztest; WST) (Schmidt & Metzler, 1992); the IPAQ (International Physical Activity Questionnaire) was employed to estimate physical activity in daily life (Booth, 2000). Additionally, the Mini International Neuropsychiatric Interview (MINI, German Version 5.0.0) (Sheehan et al., 1998) and a custom substance abuse questionnaire were conducted to rule out psychiatric symptoms and substance dependency. Moreover, the Beck Depression Inventory (BDI) (Hautzinger et al., 1994) and the trait subscale of the State-Trait-Anxiety Inventory (STAI-trait) (Spielberger et al., 1983) were collected.

Each subject underwent a preparation phase in which extensive sports medical examinations were performed to rule out health risks that would have prohibited participation in the study. Further, performance diagnostics were conducted to determine physical fitness and define individual training intensities. In the subsequent intervention phase, three exercise conditions took place in randomized order: anaerobic cycling (high-intensity), aerobic cycling (low-intensity), and a rest (control) condition. These were at least seven days apart but had to be performed within a maximum of eight weeks. On the first examination day, each subject was familiarized with a mock scanner before the actual MRI to avoid possible measurement differences due to nervousness. Otherwise, the procedures were conducted in a standardized order on each examination day. First, subjects completed the BDI and a custom questionnaire capturing current fatigue, pain, sleep duration and quality, and caffeine and alcohol consumption. Subjects were asked to get adequate sleep the night before the examination, not to drink alcohol 24 h before the examination, and not to consume caffeine until 2 h before the examination. They were also instructed not to exercise 24 h beforehand and not to engage in high-intensity exercise the day before testing. Further, questionnaires capturing mood (PANAS (Krohne et al., 1996)) and anxiety (STAI state) were acquired, as well as the Mood-Meter (Kleinert, 2006; Wollseiffen et al., 2016), a German questionnaire assessing the effects of exercise on perceived physical state, psychological strain, and motivational state. Moreover, neuropsychological tests

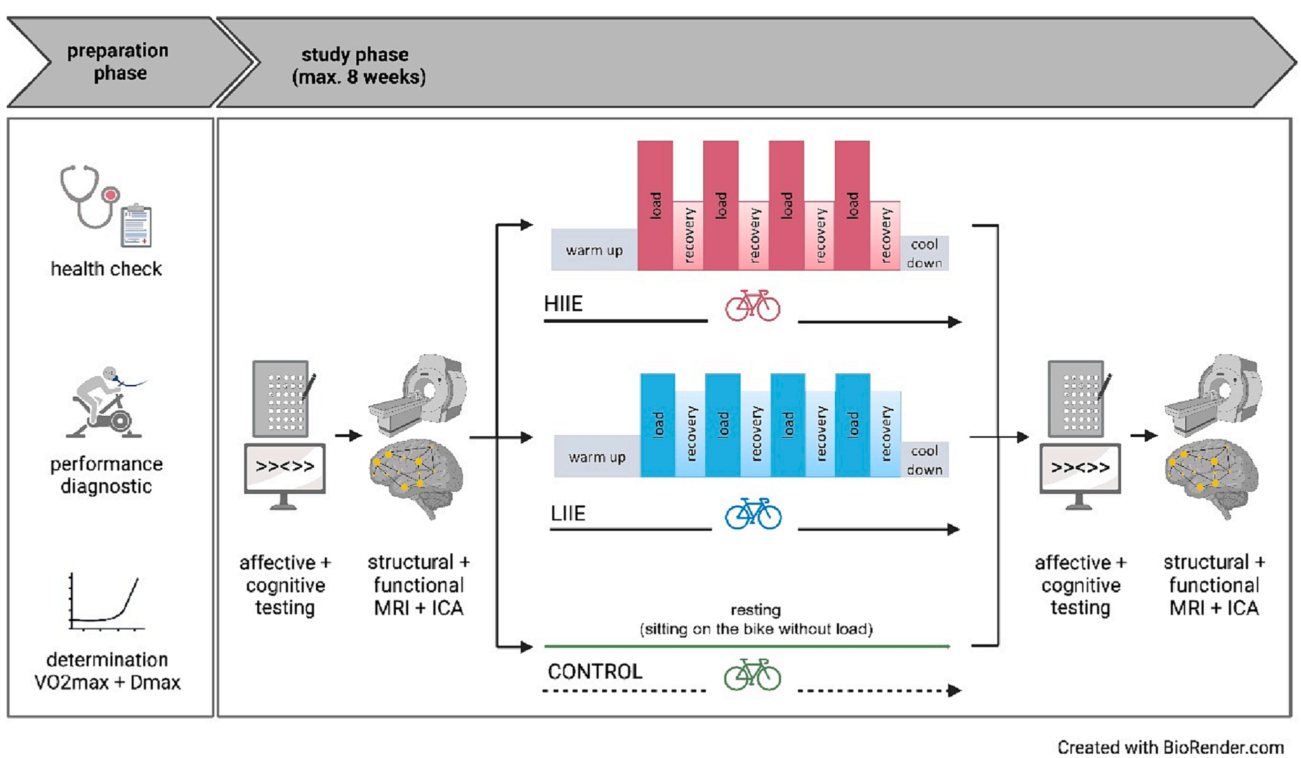

Fig. 1. Study design. HIIE = High-Intensity Interval Exercise; LIIE = Low-Intensity Interval Exercise.

capturing object recognition memory performance/hippocampal integrity using the Mnemonic Similarity Task (MST) (Stark et al., 2019) and EF using a short version of the Attention Network Test (ANT) (Weaver et al., 2013) were performed. Then, a fMRI scan was completed and, subsequently, one of the three exercise sessions. After the exercise sessions, mood questionnaires, cognitive testing, and fMRI were repeated in the same order as pre-intervention.

The present work relates solely to the influence of acute exercise of varying intensity on the RSNs and the ANT. Other manuscripts will focus on different aspects of the study. Therefore, statistics of some background variables (e.g., demographics, exercise physiological parameters, exhaustion, and HR_{rest}) are also reported in related manuscripts (e.g., Boecker et al., 2024).

2.2.2. Medical examination and incremental step test

Medical sports examination included an anamnestic questionnaire, lung and cardiac auscultation, and a 12-lead resting ECG. Where necessary, an additional transthoracic echocardiogram was carried out. Performance diagnostics consisted of a maximal incremental step test on a cycling ergometer (Cyclus2, RBM Elektronik-Automation GmbH, Leipzig, Germany), which allowed mounting each subject's racing bike to ensure the same individual and optimized cycling position for each subject throughout the study. The incremental step test started with an initial workload of 100 W and 20 W increments every 3 min at a cadence $\geq$ 80 revolutions per minute (rpm) until volitional exhaustion. Power was digitally controlled using direct drive during the performance diagnostics and the following exercise sessions. Subjects were prohibited from strenuous exercise or drinking alcohol the last 24 h before the performance diagnostic. They were instructed to refrain from caffeine and food two hours before exercise testing. The test was terminated when the cadence decreased below 65 rpm. Oxygen uptake (VO_2), metabolic respiratory quotient (respiratory exchange ratio; RER), heart rate (HR) (using Cortex meta-analyzer 3B, Leipzig, Germany, and Polar Electro Oy, Kempele, Finland), and an ECG (using Cardio 100 USB, Ergoline GmbH, Bitz, Germany) were continuously recorded during the test. HR variability was also continuously recorded using a validated Polar H10 chest strap. Further, blood pressure was measured during each stage. To determine lactate concentration, 20 µl of capillary blood was taken from the earlobe in the last 15 s of each step and directly mixed with 1 ml system hemolysis solution and analyzed amperometric-enzymatically using a EBIOplus device (EKF Diagnostic Sales, Magdeburg, Germany). Rating of perceived exertion (RPE) was assessed using the 6 to 20 points Borg scale (6 no exertion at all, 20 maximal exertion) (Borg, 1998) within the last 15 s of each increment.

Exhaustion was considered with the attainment of at least two of the following criteria: leveling off in VO_2, RER $\geq$ 1.05, high levels of blood lactate (Bla) ($\geq$ 8 mmol/L), a perceived rate of exertion of $\geq$ 18. The $relVO_{2max}$ was defined as the highest 30 s moving average of VO_2 divided by body mass (ml/min/kg). Subjects with a VO_{2max} < 55 ml/min/kg were excluded from the study, as we were interested in investigating trained subjects. De Pauw et al. (2013) suggest that subjects with a $relVO_{2max}$ from 55 ml/min/kg and up are trained.

2.2.3. Attention Network Test (ANT)

The ANT was developed to assess different attentional domains within a single task framework, namely 'alerting,' 'orienting,' and 'executive attention' (Fan et al., 2002). The present paradigm was adapted from the brief version described by Weaver et al. (2013).

The computerized task paradigm was presented using Presentation (Version 18.2 Build 02.18.16, Neurobehavioral Systems, Inc., Berkeley, CA, https://www.neurobs.com) on a 27″ LCD screen and a viewing distance of approximately 80 cm. Each trial had a fixed total duration of 3500 ms and consisted of five phases (Fig. 2). Initially, a fixation cross was presented centrally for 400–1000 ms. Then, one of four alternative warning cue conditions was shown randomly for a fixed duration of 100 ms: i) *No cue* (i.e., fixation cross continues), ii) *central cue* (i.e., fixation cross was replaced by an asterisk), iii) *double cue* (i.e., two asterisks appeared simultaneously above and below the fixation cross), or iv) *spatial cue* (i.e., one asterisk was presented above or below the fixation cross). Following another 400 ms fixation period, a flanker stimulus was presented above or below the fixation cross for a maximum duration of 1500 ms. Subjects were instructed to indicate as quickly as possible the direction of a centrally located arrow pointing left or right by pressing the left or right arrow key on the keyboard with the index or middle finger of the right (dominant) hand, respectively. Critically, this target stimulus was flanked by two arrows on each side pointing either in the same direction (congruent) or the opposite direction (incongruent). After the participant made a response, the flanker stimulus disappeared

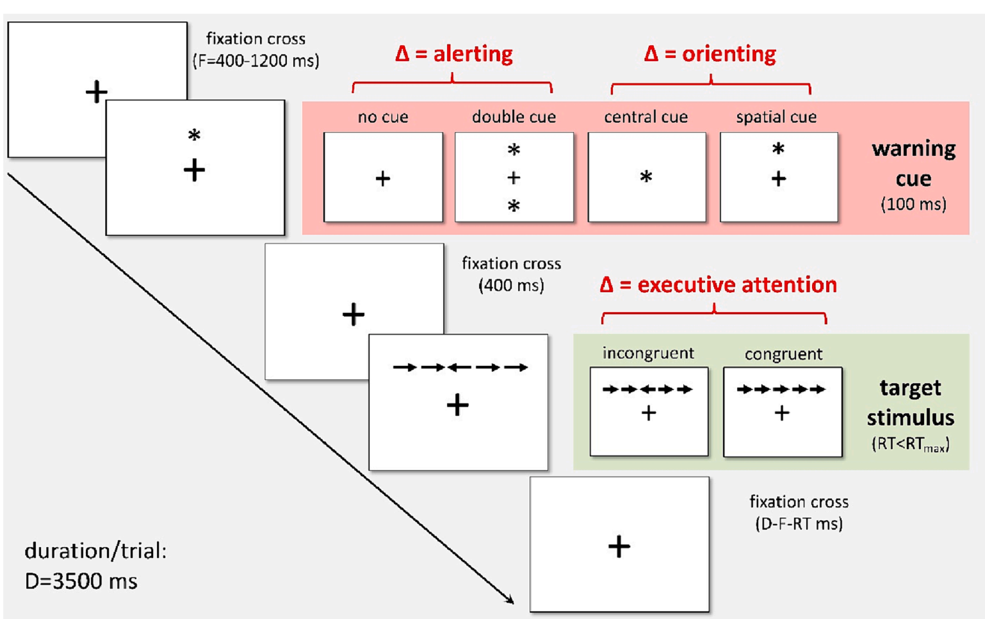

Fig. 2. Attention Network Test. Network scores were calculated as follows: alerting = $RT_{no\text{-}cue}$ - $RT_{double\text{-}cue}$; executive attention = $RT_{incongruent}$ - $RT_{congruent}$; orienting = $RT_{central\text{-}cue}$ - $RT_{spatial\text{-}cue}$. RT = Reaction time. RT_{max} = maximum delay for valid reactions.

immediately, and the fixation cross continued until the end of the trial. The reaction time (RT) and response accuracy were measured for each trial.

RT (as well as error rates) are usually higher for incongruent stimuli than congruent stimuli. This effect is referred to as the 'flanker effect' (Eriksen & Eriksen, 1974) and is used to operationalize the network of 'executive attention,' with higher mean RT differences indicating worse performance (*executive attention* = $RT_{incongruent}$ - $RT_{congruent}$) (Anzeneder et al., 2023; Kirby et al., 2015). Similar measures are widely utilized in studies (e.g., Colcombe et al., 2004) to explore acute and chronic effects of physical activity on the executive capacity for voluntary ('top-down') suppression of interfering stimuli. The four alternative cue conditions independently manipulated the other attentional network functions. Compared to no-cue trials, the presentation of central warning cues should speed up responding briefly by predicting the timing of the upcoming target. Hence, mean RT differences between no-cue and double-cue trials were used to operationalize the 'alerting' function (*alerting* = $RT_{no\text{-}cue}$ - $RT_{double\text{-}cue}$). Meanwhile, spatial cues always appeared at the spatial position of the subsequent target stimulus and could further speed up responding by eliciting an anticipatory orientation response. Therefore, mean RT differences between central-cue and spatial-cue trials were used to operationalize the 'orienting' network (*orienting* = $RT_{central\text{-}cue}$ - $RT_{spatial\text{-}cue}$). Here, larger alerting or orienting scores indicate better cognitive performance (Anzeneder et al., 2023; Kirby et al., 2015).

This test version included 16 practice trials and 160 test trials. Feedback (correct or incorrect) was provided after each practice trial but not on the test trials. The order of the trial types was random.

2.2.4. MRI acquisition

Magnetic resonance imaging was performed at the Department of Diagnostic and Interventional Radiology at University Hospital Bonn using a 3 T clinical MRI System (Ingenia Elition 3.0 T, Philips Healthcare, Best, the Netherlands) with a 32-channel head coil. Within each run, high-resolution T1-weighted (T1w) structural MRI scans were acquired for anatomic reference using a 3D-MPRAGE sequence with the following parameters: slice orientation: sagittal, sequence type: 3D FFE, acquisition matrix: 356 × 356, acquired voxel size: 0.7 × 0.7 × 0.7 mm, reconstructed voxel size: 0.49 × 0.49 × 0.57 mm, field of view (FOV): 250 × 250 × 190 mm, time of repetition (TR): 10 ms, echo time (TE): 4.7 ms, flip angle: 8°, total scan duration: 6:19 min.

Rs-fMRI data were acquired using a T2*-weighted gradient-echo, echo-planar imaging (EPI) sequence with 585 volumes and the following specifications: TR = 1020 ms, TE = 30 ms, acquired voxel size = 2.5 × 2.5 × 2.5 mm, reconstructed voxel size = 2.17 × 2.17 × 2.5 mm, FOV = 208 x 208 x 143 mm, flip angle = 52°, SENSE: 2, MB factor: 3, EPI factor: 41, matrix: 84 × 82, slices: 51, scan order: FH (ascending), duration: 10:04 min. The fMRI data were acquired parallel to the anterior-posterior commissural plane. During all rs-fMRI scans, subjects were instructed to keep their eyes closed, not to think about anything specific, and not to fall asleep.

Field mapping was performed with the following parameters: TR = 650 ms, TE = 7 ms, acquired voxel size: 3.75 × 3.75 × 4 mm, flip angle: 80°.

In addition, several structural acquisitions were recorded after the first day of intervention, which are not included in this substudy.

2.2.5. Endurance exercise sessions

Subjects underwent two experimental exercise sessions with different exercise intensities (low-intensity and high-intensity conditions) and a control condition (without load) in a randomized order (for randomization, an adapted Latin Square was used with the following intervention combinations: ABC, ACB, BCA, BAC, CBA, CAB; combinations have additionally been randomized within blocks of 6 subjects). Exercise sessions were set as High- or Low-Intensity Interval Exercises (HIIE or LIIE) with a 4*4-min load alternating with 3 min of active recovery. Individual exercise intensities were prescribed using lactate thresholds measured individually during performance diagnostics. Lactate thresholds were determined using i) first rise and ii) modified D_{max} method (Zwingmann et al., 2019). The first rise defines the point before the lactate concentration increases ≥ 4 % of the peak lactate concentration between two points on the lactate curve. The modified D_{max} defines the point with the maximal perpendicular distance of the lactate curve from a line connecting the first rise and the endpoint of the lactate curve. In both exercise conditions, subjects started with a 10-minute warm-up at 1.5 W per kilogram of body weight (W/kg BW), followed by the interval training and a final cool-down of 5 min < 1.5 W/kg BW.

Exercise intensities were structured as follows: i) LIIE: 4 * 4 min load at 100 % first rise (W) alternating with 3 min active recovery at 90 % of first rise; ii) HIIE: 4 * 4 min load at 110 % D_{max} (W) alternating with 3 min active recovery at 60 % of D_{max}, and iii) control intervention: no load while sitting on the cycling ergometer for 43 min (equal duration to an intervention).

After each load and recovery interval, blood lactate, HR_{int}, and RPE were determined in the last 30 s of each interval. Blood pressure was measured before and after the intervention. The exercise sessions were supervised and controlled.

2.3. Statistical analysis of physiological and behavioral data

Statistical analyses of the endurance exercise intervention data, the physiological data recorded during the fMRI scan, and the ANT were performed using IBM SPSS 28 (SPSS Inc., Chicago, Illinois). Significance was set at $p < 0.05$; effect sizes are given as Cohen's d.

2.3.1. Endurance exercise session

For the variables HR_{int}, lactate concentration, and RPE, paired t-tests with Bonferroni correction were calculated to examine significant differences in exercise intensity between the LIIE and HIIE conditions.

2.3.2. ANT

An LME model with time and condition as fixed effects was used to analyze variables for alerting, orienting, executive attention, accuracy, and the mean RT across all categories. The covariates exhaustion and HR_{rest} from the fMRI measurement (as fixed effects) and a random intercept were added to perform the analysis analog to the analysis of the fMRI data. In case of significant main effects or interactions, post-hoc paired t-tests with Bonferroni correction were performed.

2.3.3. Resting HR during fMRI (HR_{rest})

A pulse oximetry sensor was placed on the index finger to monitor HR (HR_{rest}) throughout each fMRI scan continuously. After removing outliers (values deviating ± 2.5 SD from the mean), a mean for the whole scanning time was calculated. With time and condition acting as fixed effects and a random intercept, an LME model was used to analyze the outlier-corrected means statistically. Post-hoc paired t-tests using the Bonferroni correction were carried out in case of significant main effects or interactions.

2.3.4. Exhaustion

To evaluate exhaustion before and after the intervention, we used a subscale of the MoodMeter consisting of the items 'feeble' and 'drowsy,' with higher scores signifying higher exhaustion. We used an LME model with time and condition as fixed effects and a random intercept for statistical analysis. In case of significant main effects or interactions, post-hoc paired t-tests with Bonferroni correction were performed.

2.4. fMRI data analysis

2.4.1. fMRI data preprocessing

A visual quality check of the MRI data was performed using MRIQC

(Esteban et al., 2017). The fMRIPrep 20.2.6 toolbox (Esteban et al., 2019) based on Nipype 1.7.0 (Gorgolewski et al., 2011) was used for further quality control and standardized preprocessing. Details of the individual preprocessing processes can be found in the Supplementary Material, which contains the automatically generated boilerplate text from fMRIPrep, with the intention that users should copy and paste it unchanged into their manuscripts. It is published under the CC0 license. Preprocessing included head motion correction, susceptibility distortion correction, coregistration of BOLD and T1w data, and normalization. Anatomical data and BOLD time series were normalized to standard space (ICBM 152 Nonlinear Asymmetrical template version 2009c; TemplateFlow ID: MNI152NLin2009cAsym; (Fonov et al., 2009)). Further quality controls were determined using the values for derivate of root mean square variance over voxels (DVARS) and framewise displacement (FD) determined by fMRIPrep. Subjects were excluded from the final analysis if more than 60 % of 585 volumes had an FD greater than 0.2 mm (Parkes et al., 2018). The five most important CSF and WM aCompCor components, 12 motion parameters, and cosine functions were used to further denoise the preprocessed data. Using the 3dTproject function from the AFNI library (https://afni.nimh.nih.gov/pub/dist/doc/program_help/3dTproject.html), noise regression and smoothing (4 mm of FWHM) were performed in a single step.

2.4.2. Independent component analysis and creation of FC maps

Using FSL MELODIC (Multivariate Exploratory Linear Optimized Decomposition into Independent Components, Version 3.15), the preprocessed data was decomposed into 45 data-driven independent components (Beckmann & Smith, 2004). Following network identification was based on the spatial similarity to functional networks described in earlier studies (Rajab et al., 2014; Schmitt et al., 2019; Smith et al., 2009; Weng et al., 2017). To objectify the identification of RSNs, a cross-correlation was calculated between the group independent component analysis (gICA) components and templates of RSN contained in two well-established RSN template approaches (Doucet et al., 2019; Yeo et al., 2011). ICA components showing maximum correlation with the networks included in the templates were selected. In contrast to the CAREN (Consensual Atlas of Resting-state Networks (Doucet et al., 2019)), we split the Central Executive Network / Frontoparietal Network (FPN) into a left and right FPN, as reported in previous literature (Smith et al., 2009), which was more in line with our gICA components. We also divided the Visual Network into a primary and secondary network. In addition to Doucet et al. (2019) and Yeo et al. (2011), we identified a Cerebellar Basal Ganglia Network (CBN), which has been described several times in the current literature (Schmitt et al., 2019; Smith et al., 2009).

In total, we identified 10 RSNs (**Supplementary Figure S1**): i) Default Mode Network (DMN); ii) Dorsal Attention Network (DAN); iii) Salience Network (SAL); iv) Executive Control Network (ECN); v) Sensorimotor Network (SMN); vi) CBN; vii) Left Frontoparietal Network (LFPN); viii) Right Frontoparietal Network (RFPN); ix) Primary Visual Network (PVN); x) Secondary Visual Network (SVN).

The selected networks were thresholded ($Z > 2.3$) and binarized. Afterward, the mean time series of each network was extracted. The dual-regression approach was used to create individual functional connectivity maps (FCmaps) for each network (Beckmann et al., 2009).

2.4.3. Linear mixed effects model

For statistical analysis, individual FCmaps for each network were analyzed using AFNI's 3dLMEr toolbox (Chen et al., 2013). Covariates age, relVO$_{2max}$, HR$_{rest}$, and exhaustion (as fixed effects) and a random intercept were added to account for random individual-level effects. Since age and relVO$_{2max}$ did not explain any further variance in the first model with four covariates, the model was reduced to two covariates only, including HR$_{rest}$ and exhaustion. Cluster correction was performed using AFNI's cluster-level FWE methods 3dFWHMx and 3dClustSim (Cox et al., 2017a, 2017b), calculating a specific cluster-defining threshold for each analysis. Significance was considered at a cluster-defining height threshold of $p < 0.001$ and an alpha level of 0.05. For further exploratory analyses, the evaluation was also repeated with a $p < 0.005$ and an alpha level of 0.05 (Saxe et al., 2018). Our primary interest were time × condition interactions. In case of significant time × condition interactions, post-hoc tests (Z-statistics) were performed. Significant clusters were labeled using AFNI's whereamI function (https://afni.nimh.nih.gov/pub/dist/doc/program_help/whereami.html) and the atlas CA_N27_ML (Eickhoff et al., 2005, 2006, 2007).

2.4.4. Correlation analysis

Further explorative analyses were performed using Spearman correlations to assess the relationship between significant rsFC changes in cognitive RSNs and behavioral data. Significance was assumed at $p < 0.05$.

3. Results

3.1. Participants

In total, 29 participants were included in this study, of which seven had to be excluded from further study participation: three subjects were excluded in the preparation phase due to insufficient fitness (relVO$_{2max}$ < 55 ml/min/kg), and four subjects needed to be excluded due to acute illness or injuries (caused by private training) that prohibited any exercise (two subjects before and two subjects after the performance diagnostics). From the resulting 22 subjects additional two subjects had to be excluded from the final analyses due to poor fMRI data quality, resulting in a final sample size of N = 20 subjects.

According to the Edinburgh Handedness Inventory, N = 19 subjects were right-hand dominant (mean laterality quotient 76.9 ± 22.4; values > +40 indicate right-handedness), and N = 1 participant was ambidextrous (laterality quotient: 29.41; values between -40 and +40 indicate ambidexterity). There was no evidence of psychiatric symptoms in any of the 20 subjects assessed by the MINI, BDI, and STAI trait. The average verbal intelligence quotient was 108.1 ± 5.8, indicating normal verbal intelligence for all subjects. Using the IPAQ, N = 19 participants could be categorized as highly active. N = 1 subject was classified as moderately active. Table 1 shows a summary of the demographic data of the cohort.

3.2. Endurance exercise session

All subjects could complete the HIIE and LIIE at the individually specified power levels (**Supplementary Table S1**). The statistical analyses revealed significant differences in HR$_{int}$, lactate concentration, and

Table 1
Cohort demographics and characteristics.

Variable	N = 20
Age [years]	27.3 ± 3.6
Height [cm]	181.6 ± 6.3
Weight [kg]	76.3 ± 6.5
BMI [kg/m^2]	23.1 ± 1.1
HR$_{peak}$ [bpm]	194.4 ± 6.8
relVO$_{2max}$ [ml/min/kg]	58.5 ± 3.5
BDI	1.6 ± 1.5
STAI trait	28.7 ± 3.5

Data are presented as mean ± standard deviation. BDI = Beck Depression Inventory (score < 11: no depression); BMI = body mass index; bpm = beats per minute; HR$_{peak}$ = maximum heart rate reached during the performance diagnostics; relVO$_{2max}$ = maximum oxygen consumption relative to body weight; STAI trait = trait anxiety of the State-Trait Anxiety Inventory (range: 20 = "not being afraid" to 80 = "maximum intensity of anxiety").

RPE between the HIIE and LIIE (**Supplementary Table S2**).

3.3. Resting HR during fMRI (HR_{rest})

Statistical analyses of HR_{rest} revealed a significant main effect of condition ($F(2, 95) = 10.31$, $p < 0.001$), a main effect of time ($F(1, 95) = 4.30$, $p = 0.041$), and a significant time × condition interaction ($F(2, 95) = 12.20$, $p < 0.001$). Post-hoc tests revealed a significant increase in HR_{rest} after HIIE (pre: 52.03 ± 6.64 bpm; post: 58.99 ± 6.95 bpm) and a decrease after the control condition (pre: 52.49 ± 8.37 bpm; post: 48.73 ± 9.01 bpm; see Table 2 for statistical details). There was no significant difference in HR_{rest} after the LIIE condition (pre: 52.45 ± 7.71 bpm; post: 54.77 ± 9.49 bpm). In addition, there were significant differences in HR_{rest} changes (delta = post-pre; delta HIIE: 6.96 ± 6.60 bpm; delta LIIE: 2.32 ± 6.30 bpm; delta control: −3.75 ± 3.12 bpm) between the HIIE and the control condition and between the LIIE and the control condition. The differences in HR_{rest}-changes between the HIIE and the LIIE conditions were nonsignificant.

3.4. Exhaustion

Descriptively, slight differences in exhaustion were observed between the conditions and pre-post-exercise (HIIE: pre: 1.65 ± 1.33, post: 1.08 ± 1.02, delta: −0.58 ± 1.21; LIIE: pre 1.03 ± 1.21, post: 0.63 ± 0.76, delta: −0.40 ± 1.23; control: pre: 1.28 ± 1.22, post: 1.20 ± 1.13, delta: −0.08 ± 1.04). Statistical analyses of exhaustion revealed a significant main effect of condition ($F(2, 95) = 4.079$, $p = 0.020$), a main effect of time ($F(1, 95) = 4.737$, $p = 0.032$) but no significant time × condition interaction ($F(2, 95) = 0.830$, $p = 0.439$). Post hoc tests revealed no significant comparisons (post vs. pre or between conditions) after Bonferroni correction (see Table 2 for statistical details).

3.5. ANT

Neither the alerting, orienting, or executive attention scores nor the evaluation of accuracy and RT showed significant main effects of time, condition, or significant time × condition interactions. Presentation of the results can be found in the **Supplement** (**Figure S2**, **Table S3**).

3.6. Functional connectivity

3.6.1. Left Frontoparietal Network (LFPN)

Within the LFPN, a significant time × condition interaction was observed in the left superior frontal gyrus (SFG) (Fig. 3, Table 3). No main effects (time or condition) were found.

Post-hoc tests revealed decreased rsFC pre to post HIIE in the left SFG and left inferior frontal gyrus (IFG; p. orbitalis). Further, a significant difference in rsFC in the left SFG was found comparing HIIE to LIIE conditions (driven by a decrease in rsFC after HIIE and an increase in rsFC after LIIE). In an extended exploratory analysis with a more lenient cluster-defining height threshold of $p < 0.005$ and an alpha level of 0.05, post-hoc tests additionally revealed a significant difference in rsFC in the left middle frontal gyrus (MFG) comparing the conditions HIIE and control, which was driven by a decrease in rsFC after HIIE and an increase in rsFC after the control condition (although both not significant when comparing pre to post within each condition) (Table 4 and **Supplementary Figure S3**).

Table 2
Statistical post hoc analysis (paired *t*-test) of HR_{rest} and exhaustion.

	p-value	T-value	df	Cohen's d
HR_{rest}				
HIIE post - pre	<0.001	4.715	19	1.054
LIIE post - pre	0.696	1.646	19	0.368
control post - pre	<0.001	−5.378	19	−1.202
delta HIIE - delta LIIE	0.354	2.007	19	0.449
delta HIIE - delta control	<0.001	6.846	19	1.531
delta LIIE - delta control	<0.001	4.500	19	1.006
Exhaustion				
HIIE post - pre	0.278	−2.132	19	−0.477
LIIE post - pre	0.975	−1.453	19	−0.325
control post - pre	1.000	−0.322	19	−0.072
delta HIIE - delta LIIE	1.000	−0.545	19	−0.122
delta HIIE - delta control	1.000	−1.385	19	−0.310
delta LIIE - delta control	1.000	−0.882	19	−0.197

P-value = Bonferroni-corrected p-value.

3.6.2. Dorsal Attention Network (DAN)

Within the DAN, a significant time × condition interaction was observed, yet at a more lenient cluster-defining height threshold of $p < 0.005$ and an alpha level of 0.05, namely in the right superior parietal lobule (SPL) (Fig. 3, Table 4). No main effects (time or condition) were found.

Post-hoc tests revealed a significant difference in rsFC between the exercise conditions in the right SPL when comparing HIIE to LIIE, which was driven by decreased rsFC from pre to post HIIE condition and increased rsFC from pre to post LIIE condition (although both changes in rsFC were not significant when comparing pre to post within each condition: **Supplementary Figure S4**). In addition, post-hoc tests showed decreased rsFC in the right MFG from pre to post HIIE condition. Further, a significant increase in rsFC was observed from pre to post LIIE condition in the left inferior parietal lobule (IPL) and the right IFG (p. opercularis). Seven other clusters showed a significant difference in rsFC between the exercise conditions comparing the HIIE and LIIE located in the following brain areas: the left SPL, the left and right IPL, the left and right MFG, the right SFG, and the right IFG (p. opercularis). These effects were driven by a decrease in rsFC after the HIIE condition and an increase in rsFC after the LIIE condition (although both not significant when comparing pre to post within each condition).

3.6.3. Cerebellar Basal Ganglia Network (CBN)

Within the CBN, a significant time × condition interaction was observed at a cluster-defining height threshold of $p < 0.005$ and an alpha level of 0.05, namely in the right cerebellum (Crus 1 and 2) (Fig. 3, Table 4). No main effects (time or condition) were found.

Post-hoc tests revealed decreased rsFC in the same brain areas from pre to post in the HIIE condition and increased rsFC from pre to post LIIE condition. Comparing HIIE to LIIE showed a significant difference between conditions in rsFC again in the right cerebellum (Crus 1 and 2) and the left cerebellum (Crus 1/2 and Crus 1/VI). Another cluster showed a significant decrease in rsFC comparing the HIIE to the control condition, namely the right cerebellum (VII/Crus 2), which was driven by a decrease in rsFC after HIIE and an increase in rsFC after the control condition (although both not significant when comparing pre to post within each condition: **Supplementary Figure S5**).

3.6.4. Other networks

Within the other networks, no significant time × condition interactions or main effects of time or condition were found for any applied thresholds.

3.7. Correlation analysis

Correlation analyses were performed between the SPL cluster of the DAN and the orienting score and the SFG cluster of the LFPN and the executive attention score, respectively. A significant correlation was identified between the beta values of the SPL peak cluster and the orienting score in the LIIE condition ($r = 0.549$; $p = 0.012$; **Supplementary Figure S6**), but not for the other conditions and not for the SFG.

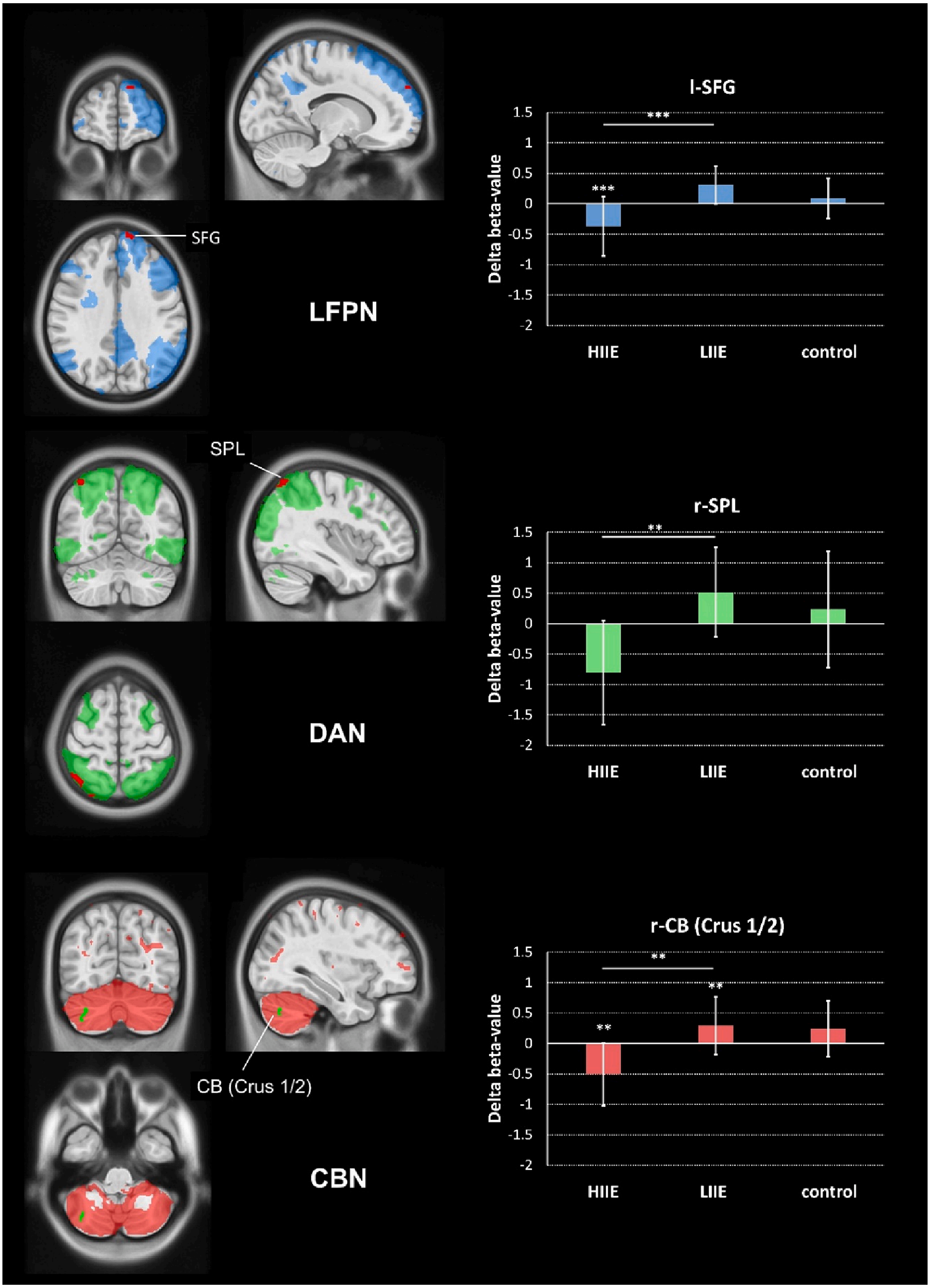

Fig. 3. Clusters with significant rsFC changes in the time × condition interaction. Significant clusters are found: i) in the LFPN in the left superior frontal gyrus (SFG) ($p < 0.001$, alpha of 0.05); ii) in the DAN in the right superior parietal lobule (SPL) ($p < 0.005$, alpha of 0.05); iii) in the CBN in the right cerebellum (CB) Crus 1/2 ($p < 0.005$, alpha of 0.05). l = left; r = right; whiskers indicate standard deviation.

4. Discussion

This within-subject crossover design study in young, trained endurance athletes aimed at investigating the influence of exercise intensity on RSNs and cognitive performance. Findings provide partial evidence for inverted U-shaped relationships between exercise and brain physiological changes as a basis for a dose-dependency of physical activity on cognition. Although we did not observe significant behavioral effects in

Table 3
Peak voxels and brain regions of significant clusters (cluster-defining height threshold of $p < 0.001$; alpha level of 0.05) with rsFC change post-exercise.

contrast	brain region	side	k	peak voxel x	y	z	Direction of change ↑/↓
LFPN							
Time x Condition	SFG	L	9	−14	60	34	
HIIE post > pre	SFG	L	9	−18	56	42	↓
	IFG (p. orbitalis)	L	10	−47	30	−8	↓
HIIE > LIIE	SFG	L	14	−10	65	37	↓

Coordinates shown are in MNI space; ↑ = increase of rsFC; ↓ = decrease of rsFC; IFG (p. orbitalis) = inferior frontal gyrus (p. orbitalis); k = cluster size; L = left; R = right; SFG = superior frontal gyrus.

the ANT task, we identified intensity-dependent effects in rsFC in cognitive RSNs: an increase in rsFC after aerobic LIIE and a decrease in rsFC after anaerobic HIIE, compatible with inverted U-shaped relationships that were previously observed between exercise and cognitive measures. Additional exploratory correlation analyses between rsFC effects and behavioral data revealed a significant correlation between the rsFC changes within the SPL (significant cluster in the DAN) and changes in the orienting score in the LIIE (but not HIIE) condition. This is in line with cognitive facilitation effects that preferentially emerge after aerobic, but not anaerobic exercise training. Unexpectedly, no effects of exercise intensity on the functioning of EF-specific RSN and ANT behavioral outcomes were observed, especially no evidence for inverted U-shape relationships: This might be reconcilable with earlier suggestions that inverted U-shape relationships only apply to certain cognitive tasks (McMorris et al., 2016; Pontifex et al., 2019), which may extend to brain physiological networks.

Exercise physiological analyses of the exercise sessions revealed significant differences in HR_{int}, lactate, and RPE between the acute exercise interventions, ensuring that two exercise conditions were performed at different intensities. As expected, we found no significant effects after the control condition, ruling out mere repetition effects after the HIIE and LIIE conditions.

Contrary to our hypothesis, we did not find significant changes in cognitive performance in the behavioral analysis of the ANT paradigm, neither for LIIE nor HIIE. Therefore, no further support for linear or curvilinear associations between exercise intensity and cognitive after-effects was found, as they were reported in previous studies (e.g., Ko et al., 2023), even though the descriptive pattern of response time changes for 'alerting' and 'orienting' (**Supplementary Figure S2**) would generally align with an inverted U-shape function. Especially with regard to the HIIE condition, this negative finding adds to the existing variability in previous studies, which showed improvements, impairments, and no changes in cognitive performance after exercise (Sudo et al., 2022). Regarding the ANT specifically, one study (Huertas et al., 2011) indicated a selective modulation of alerting (which was significant for moderate but not intense exercise). Meanwhile, a later electroencephalography study (Chang et al., 2015) observed modulation of the behavioral executive attention network score after acute moderate-intensity exercise, although modulation of P3 amplitudes for event-related potentials suggested an increased resource allocation to task-relevant stimuli for both the 'executive' and 'alerting' network. Both studies recruited slightly larger samples, which may have increased their chances of detecting systematic effects (see: Limitations), but task characteristics (e.g., duration, response modality, timing) may also play a role: For example, a recent study (Tari et al., 2023) with comparable sample size observed significant improvements in oculomotor anti-saccade performance following moderate-intensity exercise, for at least 30 min, indicating that detection of exercise effects on EF-related

Table 4
Peak voxels and brain regions of significant clusters (cluster-defining height threshold of $p < 0.005$; alpha level of 0.05) with rsFC change post-exercise.

contrast	brain region	side	k	peak voxel x	y	z	Direction of change ↑/↓
LFPN							
Time x Condition	SFG	L	25	−14	60	34	
HIIE post > pre	SFG	L	21	−18	56	42	↓
	SFG	L	20	−10	65	37	↓
	IFG (p. orbitalis)	L	20	−51	21	−8	↓
HIIE > LIIE	SFG	L	50	−10	65	37	↓
HIIE > control	MFG	L	19	−51	47	0	↓
DAN							
Time x Condition	SPL	R	41	34	−74	59	
HIIE > LIIE	SPL	R	83	38	−63	62	↓
HIIE post > pre	MFG	R	35	31	19	62	↓
LIIE post > pre	IPL	L	44	−51	−46	59	↑
	IPL	L	31	−36	−65	51	↑
	IFG (p. opercularis)	R	20	55	19	34	↑
HIIE > LIIE	SPL	L	43	−29	−76	56	↓
	IPL	L	35	−49	−50	59	↓
	IPL	R	30	57	−46	54	↓
	MFG	R	28	49	43	23	↓
	MFG/SFG	R	26	31	17	62	↓
	MFG	L	23	−32	10	65	↓
	IFG (p. opercularis)	R	22	55	19	34	↓
CBN							
Time x Condition	Cerebellum (Crus 1/2)	R	25	31	−68	−36	
HIIE post > pre	Cerebellum (Crus 2/1)	R	18	31	−70	−39	↓
LIIE post > pre	Cerebellum (Crus 2/1)	R	13	23	−83	−36	↑
HIIE > LIIE	Cerebellum (Crus 2/1)	R	30	31	−70	−39	↓
	Cerebellum (Crus 1/2)	L	17	−51	−70	−31	↓
	Cerebellum (Crus 1/VI)	L	14	−32	−65	−28	↓
HIIE > Control	Cerebellum (VII/Crus 2)	R	25	38	−65	−48	↓

Coordinates shown are in MNI space; ↑ = increase of rsFC; ↓ = decrease of rsFC; IFG (p. opercularis) = inferior frontal gyrus (p. opercularis); IFG (p. Orbitalis) = inferior frontal gyrus (p. orbitalis); IPL = inferior parietal lobule; k = cluster size; L = left; MFG = middle frontal gyrus; R = right; SFG = superior frontal gyrus; SPL = superior parietal lobule.

task performance is generally possible in smaller samples, but with an increased risk of missing latent behavioral effects. Overall, the exact influence of moderating factors on cognitive performance after acute exercise still needs further clarification. Similarly, different study designs and exercise paradigms in terms of duration and intensity make it challenging to compare various studies. Thus, a consensus on the design of exercise interventions in future studies investigating moderating factors needs to be achieved.

Imaging analyses confirmed significant increases in rsFC in the LFPN after the LIIE intervention relative to concomitantly decreased rsFC after the HIIE intervention. RsFC changes were found in the l-SFG, the l-IFG, and the l-MFG: Overall, there was a significant decrease in rsFC after the HIIE condition and a (non-significant) increase in rsFC after the LIIE condition, revealing a significant difference between the HIIE and LIIE condition. The FPN plays an important role in EF and cognitive control, i.e., voluntary goal-directed behavior, top-down control, and cognitively demanding tasks (Chenot et al., 2021; Marek & Dosenbach, 2018; Seitzman et al., 2019). The main components of the LFPN are the dorsolateral prefrontal cortex, the inferior parietal lobule, parts of the middle temporal gyrus, and regions of the dorsomedial prefrontal cortex (Seitzman et al., 2019; Won et al., 2021). Via connections to the DAN, the FPN holds the attention and controls oculomotor processes, thus, visuospatial perceptual attention and visual orientation (Dixon et al., 2018). The SFG, as a prefrontal cortex region, is involved in executive processing and working memory (Briggs et al., 2020): lesion studies show reduced working memory capacities in patients with lesions in the left SFG (du Boisgueheneuc et al., 2006). The SFG has extensive connections within the FPN and links to the DMN, motor control networks, and executive networks (Briggs et al., 2020; Li et al., 2013).

Explorative analyses with a more liberal significance threshold (cluster-defining height threshold of $p < 0.005$) revealed similar changes in rsFC in the DAN and the CBN within cognitive brain regions (decreases in rsFC after the HIIE condition and increases in rsFC after the LIIE condition). Significant clusters were found within the DAN in parietal and frontal regions of the network, particularly in the SPL, IPL, and MFG. As in the LFPN, there was a decrease in rsFC after the HIIE and an increase in rsFC after the LIIE condition. The DAN is involved in the top-down selection of stimuli and thus assumes an important role in controlling goal-directed visuospatial attention (Corbetta & Shulman, 2002). The main regions of the network are the intraparietal sulcus and the frontal eye fields (Seitzman et al., 2019). Significant clusters in the CBN are found in the left and right cerebellum, mainly in crus 1 and 2. Again, in summary, rsFC decreased after the HIIE condition and increased after the LIIE condition. The cerebellum is known to have important functions in motor control and coordination (Bostan et al., 2013; Schmahmann, 2019). However, studies show that specific cerebellum regions, e.g., crus 1 and 2 and lobules VII and VI, are involved primarily in cognitive operations such as executive processing or attention (Koziol et al., 2014; Schmahmann, 2019; Van Overwalle et al., 2020) and have connections to the prefrontal and posterior parietal cortex and different RSNs, such as the DMN, FPN, salience network, or DAN (Bostan et al., 2013; Habas, 2021). Thus, we can show that the same intensity-dependent effects of exercise on rsFC are evident in cerebellar cognitively associated regions as in prefrontal and parietal brain regions.

The present result patterns in cognitive RSNs mirror previous behavioral studies that suggested inverted U-shape relationships between exercise intensity and cognitive performance and support observations from previous rs-fMRI studies that reported differential changes in cognition-related RSNs after moderate versus high-intensity exercise (Ko et al., 2023; Schmitt et al., 2019). Meanwhile, it is notable that no significant effects were found in other cognition-related RSNs that showed evidence for modulatory effects after moderate-intensity exercise, especially the ECN (Weng et al., 2017; see also: Schmitt et al., 2019) and DMN (yet, indicating a linear relationship: Ko et al., (2023)). Given that available physiological models of exercise-cognition interactions (e.g., catecholamine and transient hypofrontality hypothesis) would predict a special vulnerability of prefrontal brain areas (which are strongly involved in these RSNs), the lack of significant changes was unexpected, although it aligns with negative findings in similar ICA-based analyses (Rajab et al., 2014).

Finally, while there were no significant behavioral effects overall, the observation of a positive correlation between rsFC increases in the right SPL (as part of the DAN) and better orienting scores in the LIIE condition provides additional, yet exploratory, evidence that low, but not high, exercise intensity is beneficial, at least for certain aspects of cognitive processing (here: visuospatial attention). This is also similar to Ko et al. (2023) who observed associations between changes in posterior cingulate to medial prefrontal cortex connectivity and behavioral performance in a mental rotation task (as an indicator for visuospatial attention): However, the moderate and the high-intensity exercise conditions in that study were performed in close temporal succession and may have influenced each other. Our design, with exercise conditions on separate days, can thus complement, substantiate, and extend the initial report by Ko et al. (2023).

4.1. Limitations

Although our sample size was limited to N = 20 subjects, we were able to examine six time points in a randomized trial. The sample size was based on experiences from previous ICA-based RSN studies in this area (Schmitt et al., 2019; see also Rajab et al., 2014; Ko et al., 2023). Yet, examinations of larger sample sizes and possibly alternative task paradigms with higher sensitivity will be needed to detect behavioral effects more robustly (Pontifex et al., 2019). Similarly, future studies should examine larger cohorts to investigate the influence of gender and ethnicity. Because we studied only young, trained male endurance athletes, further studies are needed to generalize our findings to populations with different ages and training statuses (Sudo et al., 2022). Despite our preselection of trained endurance athletes to avoid differences in HR_{rest} during rs-fMRI, differences between time points and conditions in HR_{rest} were apparent. However, we could account for these by including HR_{rest} as a covariate in our statistical analyses. Further studies that systematically compare training conditions from light to vigorous exercise should be performed to support further the hypothesis of an inverted U-shape curve in the exercise-cognition interaction.

5. Conclusion

Combining behavioral and rs-fMRI examinations, this study investigated the relationship between exercise intensity and cognitive performance in an acute within-subject crossover study design with three different exercise intensities (high, low, and control). Results revealed intensity-dependent rsFC changes in cognitive RSNs (i.e., increase after low-intensity and decrease after high-intensity exercise intervention), providing empirical evidence for an inverted U-shape relationship between exercise intensity and rsFC levels in cognition-related brain networks. Although no systematic after-effects on attentional functions on the group level were observed, the correlation between rsFC changes in the right SPL and the orienting score in the low-intensity exercise condition provided further, yet indirect, evidence supporting an intensity-dependent, subacute modulation of attentional brain networks which favors aerobic training regimen. Findings thus suggest aerobic exercise regimens to enhance cognitive performance, although further research is needed to substantiate and generalize these findings to other age groups and across different fitness levels.

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Institutional Review Board Statement

The study was conducted by the Declaration of Helsinki and approved by the Ethics Committee at the Medical Faculty of the Rheinische Friedrich-Wilhelms-Universität Bonn (no. 358/19).

Informed Consent Statement

Informed consent was obtained from all subjects involved in the study.

CRediT authorship contribution statement

Luisa Bodensohn: Data curation, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Angelika Maurer:** Conceptualization, Data curation, Formal analysis, Methodology, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Marcel Daamen:** Methodology, Writing – review & editing. **Neeraj Upadhyay:** Data curation, Formal analysis, Methodology, Writing – review & editing. **Judith Werkhausen:** Data curation, Investigation, Project administration, Writing – review & editing. **Marvin Lohaus:** Investigation, Project administration, Writing – review & editing, Data curation, Funding acquisition. **Ursula Manunzio:** Investigation, Writing – review & editing. **Christian Manunzio:** Investigation, Writing – review & editing. **Alexander Radbruch:** Resources, Writing – review & editing. **Ulrike Attenberger:** Resources, Writing – review & editing. **Henning Boecker:** Conceptualization, Funding acquisition, Investigation, Resources, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data can only be made available after contacting participating volunteers and obtaining their consent to submit data in anonymized form (as per ethics' approval). Depending on the decision of the volunteers, this may result in smaller samples.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.bandc.2024.106156.

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