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The Mode of Endurance Exercise Influences Changes in EEG Resting-State Graphs among High-Level Cross-Country Skiers

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ABSTRACT

BÜCHEL, D., P. Ø. TORVIK, T. LEHMANN, Ø. SANDBAKK, and J. BAUMEISTER. The Mode of Endurance Exercise Influences Changes in EEG Resting-State Graphs among High-Level Cross-Country Skiers. *Med. Sci. Sports Exerc.*, Vol. 55, No. 6, pp. 1003–1013, 2023. **Purpose:** Acute bouts of exercise influence the communication and organization of brain networks, with exercise intensity and volume regarded as key moderators. However, differences in coordination demands and limb involvement between exercise modes may also affect the communication and organization of brain networks after exercise and should be considered additionally. This study aimed to investigate the effect of mode on exercise-induced changes in electroencephalography (EEG) resting-state networks comparing running (RUN) and cross-country skating (XC). **Methods:** Fifteen male, highly trained participants were tested for peak oxygen uptake ($\dot{V}O_{2peak}$) during RUN (65.3 mL·min⁻¹·kg⁻¹) and XC (63.5 mL·min⁻¹·kg⁻¹) followed by incremental protocols at 50%, 70%, and 90% of speed at $\dot{V}O_{2peak}$ in both modes on the treadmill. After each exercise bout, 5-min resting-state EEG assessments using 64 channels were performed. Upon graph theory, small world index (SWI), clustering coefficient (CC), and path length (PL) were assessed in theta, alpha-1 and alpha-2 frequency bands. Repeated-measures ANOVA was applied to analyze the influence of exercise intensity and mode on modulations in brain network efficiency. **Results:** Main effects of mode on SWI ($P = 0.047$), CC ($P < 0.001$), and PL ($P = 0.031$) in the alpha-2 network indicated stronger modulations in network efficiency after XC. Main effects of exercise intensity in the theta network indicated modulated SWI ($P < 0.001$), CC ($P < 0.001$), and PL ($P = 0.003$) after exercise at 90% of $\dot{V}O_{2peak}$ speed. Physiological outcomes (heart rate, blood lactate concentration, and rating of perceived exertion) were influenced by intensity solely. **Conclusions:** The present study demonstrates that an acute bout of coordinatively challenging endurance exercise may affect brain networks differently compared with running. Future studies may consider exercise mode as a potential moderator in the acute interaction between exercise and the brain. **Key Words:** BRAIN NETWORKS, ELECTROENCEPHALOGRAPHY, COORDINATION, NEUROPLASTICITY, SPORTS TYPE

Participation in endurance exercise induces acute neuroplastic changes, which result in temporary modulations of brain function by means of molecular, cellular, and functional processes that eventually affect human cognition and behavior (1,2). Based on investigations of brain physiology and behavior before and after given loads of exercise, intensity has been shown to moderate the acute response of the resting brain to exercise, with the tendency toward more beneficial effects at moderate and high compared with low- and heavy-intensity exercise (3–5). These differences likely arise from differences

in metabolic pathways induced by the dose of exercise according to intensity and duration (6,7). Apart from intensity and volume, the mode of endurance exercise affects the physiological responses to exercise bouts because of differences in movement constraints, muscles involved, and muscle actions (8). Despite sports-specific factors such as involved limbs/muscles, technique, and equipment that affect movement economy (9), endurance mode has been barely investigated as a factor modulating acute exercise-induced neuroplasticity of the resting brain (10,11). In contrast to exercise-intensity where metabolic processes affect brain signaling, endurance mode is likely to alter brain function because of task-specific activation of cortical areas involved into mode-specific sensorimotor control demands (12).

Among exercise modes, cross-country (XC) skiing is unique because it requires highly developed cardiovascular capacities (13) in concert with strong whole-body motor coordination abilities (8). In particular, the combination of lower and upper body and the need for a sports-specific technique to generate propulsion (13) make XC skiing a highly demanding full-body endurance sport. Considering the central nervous

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system as the physiological origin of motor coordination, the repeated and rhythmic coordination of limb muscles—referred to as locomotion—requires the integration of somatosensory information in brain motor areas (14). Depending on task constraints, the degree of activation of these sensorimotor brain areas may change because of factors such as limbs involved (15), upper and lower limb phasic coordination (16), and balance demands (17). For XC skiing, these factors differ from running (RUN), because XC skiing i) involves upper body muscles to actively produce force output, ii) requires antiphase temporal sequencing of upper and lower limbs, iii) takes place at increased speed, and iv) requires sports-specific equipment such as skis that affect postural control. Although these differences in motor coordination across endurance exercise modes may hypothetically change allocation of cortical resources during and after exercise, it might also be suggested that they alter brain function in nonmotor brain areas after exercise (18,19).

To investigate changes in brain function, electroencephalography (EEG) serves as a mobile and noninvasive imaging technique with a high temporal resolution (20). Apart from EEG approaches that analyze brain function during movement that is particularly limited at high intensities because of movement artifacts, the analysis of the EEG resting states after exercise became a valid approach (21). Because exercise induces acute neuromodulatory processes like the release of neurotrophins (e.g., brain-derived neurotrophic factor), which mediate neural activity on the cell level (1), brain function remains affected after exercise cessation. Thus, the neurophysiological effects could also be assessed in a resting situation, after termination of an acute bout of exercise. Next to the activity of specific brain areas, the connectedness across the cortex, defined as resting-state networks (RSN), can be calculated based on temporal coherence between signals (22). RSNs are suggested to provide information on the responsiveness of the brain to external stimuli (23) and seem to change after exercise (3,5). In our previous investigations, we applied EEG to extract RSNs and were able to describe acute exercise-induced changes in brain function (5) at an acceptable level of reliability (24). In these investigations, we calculated global graph outcomes like the clustering coefficient (CC), the characteristic path length (PL), and the small-world index (SWI) to describe changes in the efficiency of brain network communication.

To date, studies have investigated the effects of exercise on the brain, applying either RUN or cycling protocols (21). Considering the physiological differences between endurance exercise modes (8), the question arises of whether associated differences in motor coordination demands influence the acute effects of exercise on brain function. A better understanding of brain responses due to sports-specific coordination demands may allow a more precise tailoring of training programs in the future. Therefore, this study aimed to investigate the influence of exercise intensity and endurance mode on exercise-induced changes in RSNs. In a laboratory study, we compared two endurance exercise modes on the treadmill with differences in motor coordination: a RUN protocol and an XC

skiing protocol with roller skis matched for intensity. To account for demands on XC skiing technique, a group of highly trained XC skiers training a similar amount of RUN and XC skiing (25,26) was tested. According to previous findings, we expected exhaustive exercise to induce detrimental changes in attention-related RSNs (5,27). With regard to differences in upper body involvement and technique between both endurance modes, we further aimed to explore the modulatory effect of exercise mode on connectivity in sensorimotor RSNs. To assess RSNs, we applied methodological approaches from previous studies (5,24). Accordingly, the findings of the present study may extend our understanding of the neuroregulatory effect of exercise with specific regard to exercise modes, including challenging upper and lower limb coordination (12). With regard to sports performance, our analyses may reveal novel insights into athlete's acute response to exercise bouts and may forward the integration of the brain into performance monitoring (28).

METHODS

Participants. We calculated a required sample size to achieve 0.8 statistical power at an alpha level of 0.05 using GPower, Version 3.1 (29), and we based assumed effect sizes on our recent publication (Büchel et al. [5]) where we observed an effect size of 0.48 of exercise intensity on brain graphs in a within-factor ANOVA design with two groups and five repetitions. This calculation led to a required participant sample size of 16. Finally, 15 healthy young male XC skiers (20.1 + 0.6 yr, 74.4 + 5.6 kg, 178.9 + 5.5 cm) participated in the present investigation. Because the menstrual cycle may cause substantial day-to-day changes in RSN organization in female participants, we preferred not to include women in this explorative study but rather examine similar aspects and the effect of menstrual cycle in follow-up studies (30). All athletes were students and competed at Norwegian national XC races and trained about 15 to 20 h·wk⁻¹ at the time of the investigation. Physiological information on the subjects performance level can be found in Table 1. Acute or chronic states of neurological diseases as well as injuries served as exclusion criteria for study participation. Before participation, athletes signed a written informed consent form in accordance with the Declaration of Helsinki. The study procedure

TABLE 1. Comparison of physiological data derived from initial aerobic capacity assessment comparing RUN and XC skiing exercise on the treadmill.

	RUN	XC	P	r
HR _{peak} (bpm)	200.4 ± 13.9	196.4 ± 15.0	<0.001	0.909
VO _{2peak} (mL·min ⁻¹ ·kg ⁻¹)	65.3 ± 4.3	63.5 ± 5.8	0.015	0.612
vVO _{2peak} (km·h ⁻¹)	14.5 ± 0.9	20.4 ± 1.5	0.011	0.633
BLA _{peak} (mmol·L ⁻¹)	11.1 ± 2.0	10.5 ± 2.7	0.060	0.496
RER (O ₂ /CO ₂ ratio)	1.2 ± 0.4	1.1 ± 0.4	0.462	0.206
50%vVO _{2peak} (km·h ⁻¹)	6.8 ± 0.4	10.2 ± 0.7	0.009	0.648
70%vVO _{2peak} (km·h ⁻¹)	9.5 ± 0.5	14.3 ± 1.0	0.009	0.648
90%vVO _{2peak} (km·h ⁻¹)	12.2 ± 0.7	18.4 ± 1.3	0.009	0.648

Data assessed include HR_{peak}, VO_{2peak}, vVO_{2peak}, BLA_{peak}, and calculated speeds at 50%, 70%, and 90% of vVO_{2peak}. P values indicate the statistical differences between both protocols, and r values indicate correlation across test variables according to Pearson.

was approved by the ethics committee of the Norwegian University of Technology and Science.

Procedures. The participants performed four experimental sessions, including i) a RUN peak oxygen uptake ($\dot{V}O_{2peak}$) test, ii) an XC skating $\dot{V}O_{2peak}$ test, iii) an individual RUN protocol with EEG assessment, and iv) an individual XC skating protocol with EEG assessment. The time between the two EEG measurements did not exceed 3 wk, and all measurements took place during the competitive phase of the season (October to February), where only minor changes in physiological parameters of highly trained XC skiers can be observed (31). Because the testing sessions needed to be fitted into the training and competition schedule of the athletes, 10 athletes started with session iii and 5 athletes started with session iv.

RUN $\dot{V}O_{2peak}$ test. The RUN $\dot{V}O_{2peak}$ test took place on a motorized treadmill (RL 2500E; Rodby, Södertälje, Sweden). To warm up, athletes performed a submaximal lactate profile starting at $8 \text{ km}\cdot\text{h}^{-1}$ and incline of 10.5% for 5 min. After each stage, a blood sample (20 μL) was taken from the fingertip, and lactate concentration was analyzed using the stationary Biosen C-Line lactate analyzer (Biosen; EKF Industrial Electronics, Magdeburg, Germany). During the protocol, speed was increased by $1 \text{ km}\cdot\text{h}^{-1}$ per stage until lactate concentration increased absolutely by $1 \text{ mmol}\cdot\text{L}^{-1}$ compared with the previous sample and passed the $4 \text{ mmol}\cdot\text{L}^{-1}$ threshold. After cessation of the submaximal lactate profile, participants performed an 8-min recovery and cool-down period. The $\dot{V}O_{2peak}$ test then started at the speed of the second last stage and was performed in an incremental manner. After every minute, the treadmill speed was progressively increased by $1 \text{ km}\cdot\text{h}^{-1}$. The test stopped at voluntary exhaustion of the participants. During the incremental test, $\dot{V}O_{2peak}$, maximum ventilation ($\dot{V}E$), and respiratory exchange rate (RER) were measured breath-by-breath using a stationary gas analysis system (VYNTUS CPX, Vyaire, Germany). $\dot{V}O_{2peak}$ was defined as the mean of the two highest and consecutive 30-s measurements. Accordingly, $v\dot{V}O_{2peak}$ was defined as the speed at the first of these two 30-s measurements. Simultaneously, heart rate was measured using an electrocardiogram sensor connected to a chest belt (HRM3-SS; Garmin, Schaffhausen, Switzerland) to define peak heart rate ($HR_{peak \text{ RUN}}$) as the maximum heart rate reached during the RUN test. Furthermore, a lactate sample was taken after cessation of the test.

XC skating $\dot{V}O_{2peak}$ test. The XC skating $\dot{V}O_{2peak}$ test took place on an oversize motorized treadmill (RL 3500E; Rodby, Södertälje, Sweden) in the laboratory. All athletes were instructed to perform the skating test utilizing the skating G3 subtechnique and used the same pair of skating-roller skis (IDT Sports, Lena, Norway) and poles adjusted for body size. Roller ski skating in the laboratory was shown to have large to very large correlations with XC skiing performance in the field (32). For warm-up, athletes performed a submaximal lactate profile starting at $10 \text{ km}\cdot\text{h}^{-1}$ and incline of 5% for 5 min. After each stage, a blood sample (20 μL) was taken from the fingertip, and lactate concentration was analyzed. The speed was increased by $2 \text{ km}\cdot\text{h}^{-1}$ per stage until lactate concentration

increased absolutely by $1 \text{ mmol}\cdot\text{L}^{-1}$ compared with the previous sample and passed the $4 \text{ mmol}\cdot\text{L}^{-1}$ threshold. After cessation of the submaximal lactate profile, participants had 8 min to recover and cool down. The $\dot{V}O_{2max}$ test then started at $10 \text{ km}\cdot\text{h}^{-1}$ and was performed in an incremental manner. After each minute, the speed of the treadmill was increased by $2 \text{ km}\cdot\text{h}^{-1}$. After reaching the speed of $20 \text{ km}\cdot\text{h}^{-1}$, the speed was increased by $1 \text{ km}\cdot\text{h}^{-1}\cdot\text{min}^{-1}$. The test stopped at voluntary exhaustion of the participants. During the incremental skating test, $\dot{V}O_{2peak}$, $\dot{V}E$, and RER were measured breath by breath. $\dot{V}O_{2peak}$ was defined as the highest average of two consecutive 30-s average values. Accordingly, $v\dot{V}O_{2peak}$ was defined as the speed where athletes reached $\dot{V}O_{2peak}$. Simultaneously, heart rate was measured to define peak heart rate skating ($HR_{peak \text{ skate}}$), and a blood sample was taken from the fingertip after cessation. An overview of the physiological outcomes revealed from aerobic assessment is presented in Table 1.

Individual XC skating and RUN protocol. To allow for comparisons between exercise modes (RUN vs XC skating), the individual exercise protocols were matched for external load based on individual $v\dot{V}O_{2peak}$. Accordingly, the protocol consisted of four exercise stages: i) RUN/XC skating at 50% $v\dot{V}O_{2peak}$ for 10 min, ii) RUN/XC skating at 70% $v\dot{V}O_{2peak}$ for 10 min, iii) RUN/XC skating at 90% $v\dot{V}O_{2peak}$ until voluntary exhaustion, and iv) RUN/XC skating at 50% $v\dot{V}O_{2peak}$ for 8 min. The cool-down exercise bout was followed by 10 min of active recovery. If the voluntary exhaustion stage lasted longer than 5 min, speed was increased by 1% $v\dot{V}O_{2peak}$ per minute after the fifth minute. Athletes performed the RUN and XC skiing protocol in a randomized order. An overview of the experimental procedure is provided in Figure 1.

Several physiological data considerations were assessed to estimate the individual exercise load during the different stages. Outcomes analyzed included the CR-20 Borg Scale of subjective rate of perceived exertion (RPE), the average and maximum heart rate during the exercise stages (HR_{mean} and HR_{peak} , respectively), and during resting states ($HR_{rest \text{ mean}}$ and $HR_{rest \text{ peak}}$, respectively), as well as blood lactate concentration based on fingertip blood samples (BLa) using the instruments introduced above.

EEG assessment. The procedures of EEG data assessment were applied according to previous EEG resting state investigations (5,24). Electrocortical activity was recorded by 65 passive wet electrodes (RNET; Brain Products, Gilching, Germany) connected to a wireless transmission system (LiveAmp; BrainProducts). Electrodes were online-referenced to FCz and attached according to the international 10–20 system. EEG recordings were obtained in a seated position with eyes open in front of a whiteboard (distance $\sim 1.5 \text{ m}$) and lasted for 5 min each. Accordingly, the EEG resting states were recorded in six situations: i) before the start of the protocol (PRE), ii) after low-intensity exercise (ACUTE1), iii) after moderate-intensity exercise (ACUTE2), iv) after exhaustive exercise (ACUTE3), v) after cool-down exercise (REG1), and vi) after 10 min of recovery (REG2). An overview of the treadmill protocol is presented in Figure 1.

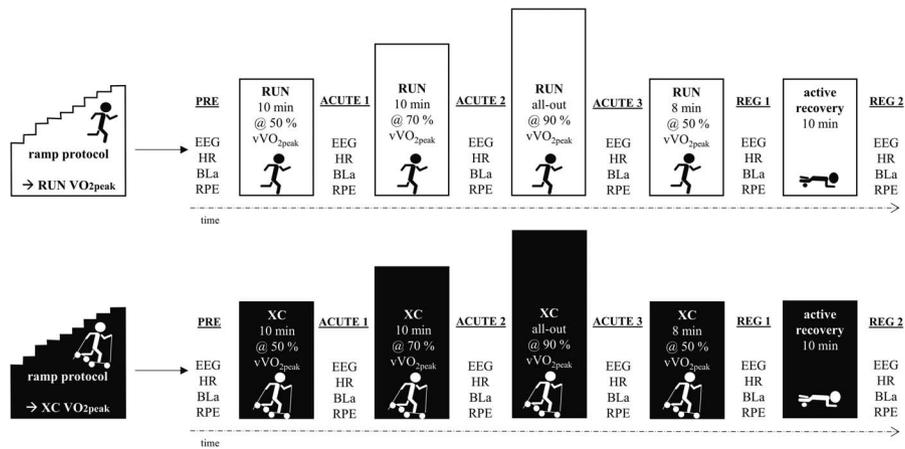


FIGURE 1—Overview of the experimental procedure to investigate the effect of exercise modality on brain graph modulation. For both RUN and XC skiing, an initial incremental treadmill test on separate days allowed $\dot{V}O_{2peak}$ to be assessed. During the experimental session, EEG resting-state data, HR, BLA, and RPE using Borg Scale 6–20 were assessed before (PRE) and after (ACUTE 1, ACUTE 2, ACUTE 3, REC 1, and REC 2) intermittent bouts of acute exercise individualized based on $v\dot{V}O_{2peak}$.

The fast applicability of the EEG wet electrodes allowed resting-state assessments to start within 4 ± 0.5 min after stage termination of the exercise stages. Before starting the recording, electrode impedances were kept below $25 \text{ k}\Omega$ for all electrodes. Because wearing an EEG cap while exercising at high intensities is not comfortable and may result in shifts of electrode placement, the cap was only applied to the participant's head during each break. To consider exercise-induced changes in heart rate during the EEG resting state, timestamps were manually set using a watch (Forerunner 935; Garmin). Before and after applying the EEG cap, sweat was removed from the hair and the interelectrode space using a towel to prevent the building of electrical bridges.

EEG preprocessing. For data processing, EEG recordings were imported into the EEGLAB toolbox v14.1.2 (33) for MATLAB (Version R2019a; MathWorks Inc., Natick, MA). The detailed steps of EEG preprocessing were reported in a recent article on exercise-induced changes in EEG brain graphs (24). These automatic processing steps included the application of i) sinusoidal line noise removal (CleanLine Plugin, Version 1.04, <http://www.nitrc.org/projects/cleanline>), ii) bandpass filtering between 3 and 30 Hz, iii) average referencing and recomputing of the reference electrode FCz, v) downsampling from 500 to 256 Hz, vi) removal of bridged channels applying the eBridge tool (34), and vii) artifact-subspace reconstruction (clean_rawdata plugin, Version 2.3, https://github.com/scen/clean_rawdata). After ASR, adaptive mixture independent component analysis (35) was applied to remove signal components from nonbrain sources like eye, heart rate, muscle, sweat, and channel noise. Finally, the clean data were epoched into sequences of 8 s with a phase overlap of 4 s (24). The first 40 epochs of each EEG resting-state recording were chosen for connectivity analysis.

Graph analysis. To compute brain graphs, we imported the epoched data to the BrainWave software (Version 0.9.151.7.255, <https://home.kpn.nl/stam7883/brainwave.html>). Functional connectivity (FC) between EEG channels

was calculated using the weighted Phase-Lag Index (wPLI). The wPLI is an index of the asymmetry in the distribution of phase differences calculated based on instantaneous phases of two time series. wPLI values can range from 0 to 1, whereas 1 represents perfect phase locking. By ignoring zero-phase interactions, phase-lag measures are stated to be less sensitive to signal amplitudes and volume conduction effects (36). The wPLI was computed on the scalp level for all possible connections between two electrodes for each epoch. Therefore, forty 65-by-65 matrices were computed for each participant per condition. The computation of wPLI was performed for the theta (5–8 Hz), alpha-1 (8–10.5 Hz), and alpha-2 (10.5 to 13 Hz) frequency bands according to Büchel et al. (5). Higher-frequency bands such as beta were not considered for the present study because of reasonable day-to-day differences observed in one of our previous investigations (24).

For the calculation of weighted, undirected brain graphs, the resulting connectivity matrices were imported to the MATLAB-based Brain Connectivity Toolbox (37). To obtain comparability despite the interindividual differences of absolute FC measures across participants, connectivity matrices were normalized, by bounding all wPLI values to the range from 0 to 1 based on the rank of the maximal and minimum values per participant. Because we did not apply an arbitrary threshold for the removal of weakly connected nodes, the weighted network approach allowed us to consider all possible connections across the scalp. The global graph measures CC, PL, and SWI were computed as outcomes of interest. Hereof, CC and PL were analyzed as global graph outcomes. The CC serves as a measure of network segregation and describes the tendency of a network to build local clusters within its direct neighborhood. PL serves as a measure of network integration and describes the average steps the given information needs to travel from any position in the network to another. The SWI serves as a measure of network efficiency and describes the relationship between short and long connections. For its computation, CC and PL were normalized by dividing each

individual value by the mean of all other values over all frequency bands. Finally, SWI was calculated as the individual ratio between normalized CC and normalized PL that was computed.

Statistical analysis. Statistical analyses were performed in SPSS 26 (SPSS Inc., Chicago, IL). All results are given as mean ± SD. Normal distribution of the data was verified by applying the Kolmogorov–Smirnov test. ANOVA for repeated measures allowed us to analyze differences between physiological outcomes and resting-state EEG data considering two given factors: MODE (RUN vs XC) and LOAD (PRE, POST1, POST2, POST3, REC1, REC2). For analysis of physiological responses, absolute values of HR (in % HR_{max}), BLa (in mmol·L⁻¹), and RPE were analyzed. For the analysis of EEG data, differences between baseline EEG before exercise at each experimental day (PRE) and POST1, POST2, POST3, REC1, and REC2 served as corresponding outcomes because we observed considerable day-to-day differences, for example, for the theta frequency band in our previous investigation (24). Because HR_{run} failed to match assumptions of normal distribution, Friedman tests of differences among repeated measures grouped for LOAD and MODE were conducted. *Post hoc* tests corrected for multiple comparison according to Bonferroni were applied in case of significant main effects, to localize effects between the different experimental conditions. The statistical

level of significance was set to $P < 0.05$. For interpretation of effect sizes, partial eta squared (η_p^2) was calculated, and 0.01, 0.06, and 0.14 were considered small, medium, and large effect sizes, respectively (38).

RESULTS

Physiological data. ANOVA for repeated measures revealed significant main effects of load on HR_{rest mean} ($F_{5,10} = 56.580, P < 0.001, \eta_p^2 = 0.802$), BLa ($F_{5,10} = 336.355, P < 0.001, \eta_p^2 = 0.96$), and RPE ($F_{3,12} = 240.533, P < 0.001, \eta_p^2 = 0.945$). For HR_{mean}, Friedman test also demonstrated significant main effects of LOAD ($\chi^2 = 119.806, P < 0.001$). All outcomes demonstrated maxima after POST3. Furthermore, Friedman test also demonstrated significant main effects of MODE ($\chi^2 = 27.74, P < 0.001$) on HR_{mean}, with higher values for XC compared with RUN. A visualization of physiological responses to exercise is provided in Figure 2.

Brain networks. ANOVA for repeated measures revealed significant main effects of LOAD on CC ($F_{4,11} = 6.085, P < 0.001, \eta_p^2 = 0.303$), PL ($F_{4,11} = 5.514, P = 0.003, \eta_p^2 = 0.247$), and SWI ($F_{4,11} = 5.514, P < 0.001, \eta_p^2 = 0.283$) in the theta frequency. *Post hoc* analysis indicated significant lower CC and SWI at POST3 compared with POST1 ($P = 0.049$ and $P = 0.028$, respectively), POST2 ($P < 0.001$

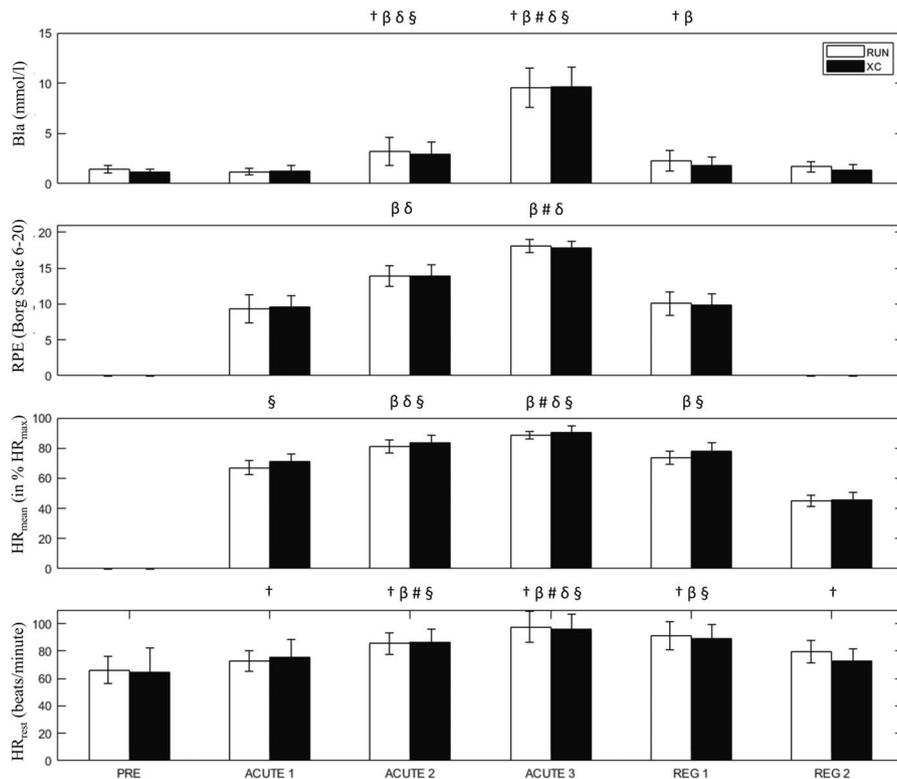


FIGURE 2—Overview of physiological responses to different exercise loads during RUN (white) and XC skiing (black) on the treadmill. Data were assessed during different acute exercise loads: before exercise (PRE), after low-intensity exercise (ACUTE1), moderate-intensity exercise (ACUTE2), exhaustive-intensity exercise (ACUTE3), cool-down exercise (REC1), and active recovery (REC2). Data include BLa, subjective RPE, mean heart rate during RUN (HR_{mean}), and mean heart rate during EEG resting state assessment (HR_{rest}). For RPE, no values were assessed at PRE and REC2. For HR_{mean}, no values were assessed at PRE. †Significantly higher than PRE. βSignificantly higher than ACUTE1. #Significantly higher than ACUTE2. *Significantly higher than ACUTE3. δSignificantly higher than REC1. §Significantly higher than REC2. Level of significance was set at $P < 0.05$.

and $P = 0.002$, respectively), and REC2 ($P = 0.024$ and $P = 0.033$, respectively). For PL, higher values were observed at POST3 compared with POST1 ($P = 0.040$) and POST2 ($P = 0.004$).

Furthermore, ANOVA revealed a main effect of MODE on CC ($F_{1,14} = 7.969$, $P = 0.014$, $\eta_p^2 = 0.363$), PL ($F_{1,14} = 5.737$, $P = 0.031$, $\eta_p^2 = 0.291$), and SWI ($F_{1,14} = 4.720$, $P = 0.047$, $\eta_p^2 = 0.252$) in the alpha-2 frequency band. Data indicated higher CC, higher SWI, and lower PL during the XC protocol compared with RUN, respectively. An overview of extracted graph measures during different exercise conditions is presented in Figures 3–5.

DISCUSSION

The present study aimed to investigate the influence of endurance exercise mode on exercise-induced changes in RSNs by applying EEG graph analysis after intensity-matched RUN and XC in highly trained XC skiers. In accordance with our hypothesis, data indicated increased modulation of efficiency in alpha-2 networks after XC skiing compared with RUN. For both endurance exercise modes, similar modulations of brain network efficiency appeared after exhaustive exercise load.

The main finding of the present investigation was an increased modulation of efficiency in alpha-2 networks after XC skating compared with RUN. Because we observed highly comparable physiological responses and subjective perception of exertion for RUN and XC skiing, we assume that the higher increases in alpha-2 network efficiency may result from the sports-specific demands of XC skating compared with the more general mode of RUN. Accordingly, increased sensorimotor demands and full-body coordination (39) in XC skating may involve more cortical resources during exercise and may therefore alter communication within the cortex after exercise.

In general, oscillations in the alpha-2 frequency band are associated with task-related information processing, as well as corticocortical and thalamocortical information flow (40). Functionally, alpha oscillations are linked to active inhibition of nonessential neuronal processing and therefore gait information flow within the brain (41). Accordingly, the degree of desynchronization in the alpha-2 band was previously associated with the complexity of task-relevant information processing (42,43) and increasing task demands during sensorimotor tasks (44). According to the assumption that cortical reallocation relies on exercise demands (18), we assume that higher demands on movement coordination during XC skating induced a greater change in the communication of task-relevant neural circuits after exercise because of concurring resources. To discriminate movement coordination between RUN and XC skating, two aspects of movement coordination might be considered: i) the role of the upper body during XC skating and ii) the complexity of movement coordination. Previous findings indicated that the simultaneous control of both arms and legs induces stronger desynchronization of alpha oscillations in brain motor areas compared with leg activity only (15). Therefore, the active involvement of the upper body to

produce propulsion during XC skiing (39) may require additional cortical resources to coordinate this movement. Furthermore, increased information flow in the alpha-2 frequency was reported in finger movement reproductions as a function of task complexity, because more complex movements evoked stronger desynchronization in motor-related brain areas (45). Because XC skating requires a precise temporal and spatial sequencing of movement between the upper and lower body (46), complexity of motor coordination during XC skating may exceed coordinative demands during RUN and require increased allocation of resources, resulting in increased corticocortical information exchange after exercise cessation (18). Consequently, the modulation of the alpha-2 network after XC skating might be interpreted as a function of coordinative demands, as more cortical resources are involved to coordinate movement during exercise.

In the current body of literature, increased small-world characteristics in the alpha-2 network were considered a long-term maladaptation of brain function after chronic diseases such as Alzheimer's disease (47) or obsessive-compulsive disorder (48). In this regard, increased small-world characteristics in the alpha-2 frequency are interpreted as a state of reduced specificity of information exchange in the resting brain (48). Because we investigated short-term responses of the brain immediately after exercise, increased alpha-2 network modulations after XC skating compared with RUN may demonstrate a temporary deterioration from "normal network efficiency," possibly arising from more complex coordination demands during preceding exercise, namely, upper body involvement and sports-specific technique.

Another observation of our study was that the efficiency in the theta network decreased significantly after the most intense exercise bout for both XC skiing and RUN. Considering that all individuals demonstrated maximal physiological responses after this exercise stage, it might be stated that exhaustive exercise load induces short-term distortions of attention-related brain networks.

Theta frequency oscillations are associated with activity in the structures of the prefrontal cortex and processes of attentional control and executive function (49). Therefore, theta frequencies are suggested to play a major role in attentional processes associated with motor coordination (50). Thus, a modulation of corticocortical communication within the theta network may be associated with an exhaustion-induced disturbance of executive brain function (5,27). In endurance modes with challenging motor coordination like XC skiing or swimming, this state of reduced network efficiency might be associated with exhaustion-induced decrements in technique (51). Because the present data revealed reduced network efficiency in the theta band for both endurance protocols, this specific pattern might be associated with exercise intensity rather than exercise mode. Therefore, the metabolic responses induced by exhaustive exercise may contribute to changes in brain network communication. Accordingly, the accumulation of metabolites was shown to interact with receptors in the brain and consequently changes brain function (52). Depending on

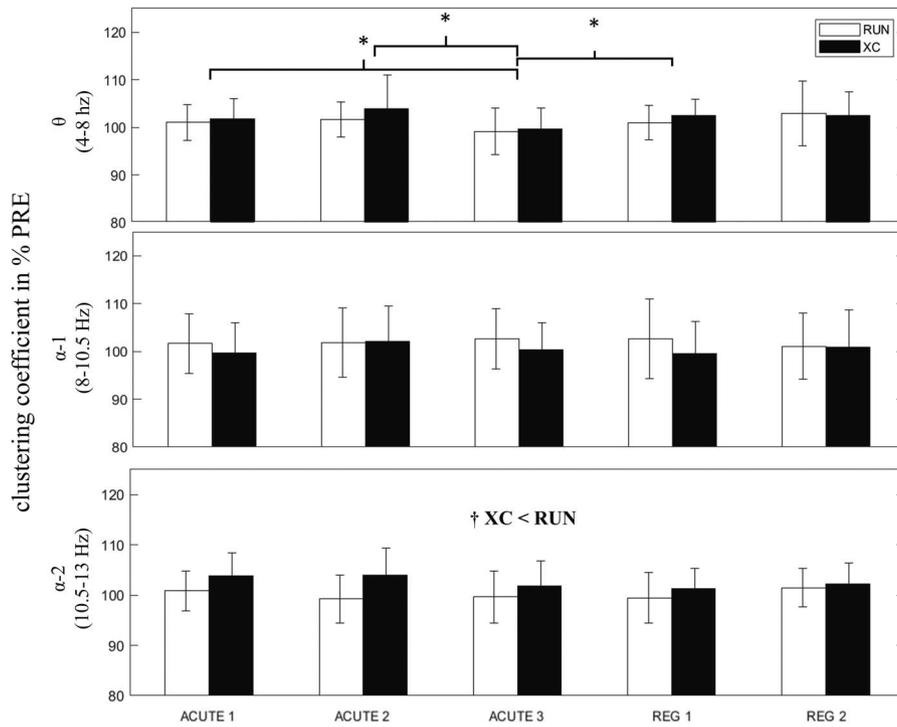


FIGURE 3—Overview of modulations of EEG resting-state CC in response to different exercise loads during RUN (white) and XC skiing (black) on the treadmill. Modulations are displayed as % delta (Δ) from PRE to postconditions regarding the calculated graph outcome in the theta (θ ; 4–8 Hz), alpha-1 (α -1; 8–10.5 Hz), and alpha-2 (α -2; 10.5–13 Hz) frequency bands. **Post hoc* differences regarding exercise intensity. †Main effects for modality. Level of significance was set at $P < 0.05$.

metabolite concentration, the excitability of neural ensembles can be affected and therefore temporarily modulate brain function (52). In agreement with our observations, Tamburro et al.

(53) extracted brain graphs from participants during graded cycling exercise and observed that facilitations of brain network efficiency appearing at moderate exercise intensity

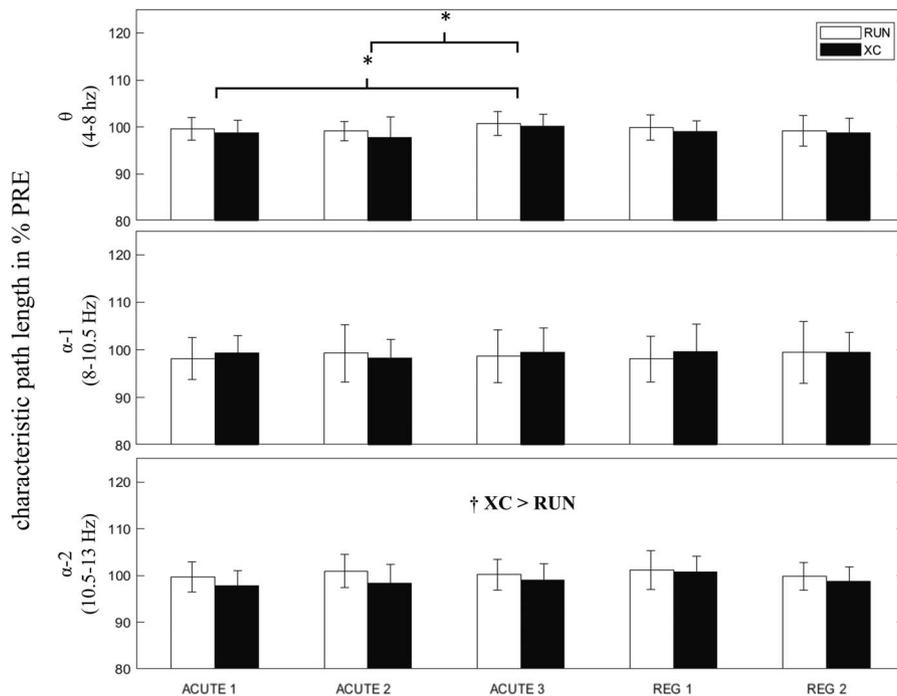


FIGURE 4—Overview of modulations of EEG resting-state characteristic PL in response to different exercise loads during RUN (white) and XC skiing (black) on the treadmill. Modulations are displayed as % delta (Δ) from PRE to postconditions regarding the calculated graph outcome in the theta (θ ; 4–8 Hz), alpha-1 (α -1; 8–10.5 Hz), and alpha-2 (α -2; 10.5–13 Hz) frequency bands. **Post hoc* differences regarding exercise intensity. †Main effects for modality. Level of significance was set at $P < 0.05$.

expertise. Therefore, it should be considered that the high training status of the investigated sample may have resulted in sample-specific modulations of brain function. To increase transferability, future investigations should consider including subgroups with different performance levels to investigate the effect of exercise mode on brain function (58), and female participants should be examined.

A further limitation was that the protocol order was not fully counterbalanced, because the experimental sessions were arranged according to the training schedule of the athletes. Therefore, more athletes started with RUN and less athletes (5 of 15) started with XC. Although the included XC athletes were familiar with the two investigated endurance modes and were regularly tested at the laboratory environment at the study site, potential limitations due to this should be considered. Despite the fact that XC skiers train high amounts in both investigated modes throughout the entire year, they prioritized skiing modes in the competitive phase of the season (13). Therefore, variations in the distribution of the exercise modes across the season may have affected the familiarization and confounded mode-specific modulations of brain function. Taken together, experimental aspects like fitness level, sex, mode counterbalancing, and exercise familiarity should be considered as potential confounders of mode-specific modulations of brain function in athletes.

Furthermore, EEG-specific limitations affect the interpretation of the obtained findings. One important limitation comes with the choice of analyzing RSN organization in the channel space because of the lower reliability of reconstructing cortical sources in repeated-measures designs (59). Thus, possible effects of volume conduction on the computed connectomes cannot be ruled out by certainty, even if the volume conduction robust wPLI was chosen. However, Miljevic et al. (60) suggested that particularly for intraindividual analysis of global graph metrics, the volume conduction of underlying sources will remain stable and should not affect the data too much, resulting in more reliable results compared with source space approaches. Another methodological issue is the contribution of exercise-induced sweating to the EEG data. Sweating

on the scalp surface increases the risk of electrical bridging and further results in slow drift artifacts contaminating the measured electrocortical potential changes. During processing, the impact of slow-drift sweating artifacts was minimized because of a high-pass filter (61), and bridged channels (0.2 ± 1.1 channels per recording) were identified and interpolated (34). In addition, the use of the wPLI as a FC metric insensitive for volume conduction and zero-lag connectivity particularly reduced the impact of electrical bridges on the FC estimation (36). However, systemic physiological responses such as sweating on noninvasive neurophysiological methods like the EEG remain complex sources of artifact and need to be considered in exercise neuroscience investigations (62).

CONCLUSIONS

The present investigation revealed insights into the role of exercise intensity and exercise mode on resting-state brain network responses to acute bouts of exercise. We observed that an acute bout of coordinatively challenging endurance exercise affects brain networks differently from an acute bout of RUN for athletes who are similarly trained in both modes. Furthermore, we observed a modulation of brain network efficiency after maximal intensity exercise bouts independent of the endurance mode performed. Therefore, we propose that future studies extend perspectives on brain–exercise interactions and consider endurance mode a moderator of brain network responses. This may allow training programs to be tailored in the context of prevention, rehabilitation, and high performance by stimulating specific physiological adaptations to exercise, including those of the brain.

The authors declare no conflict of interest. The results of the study are presented clearly, honestly, and without fabrication, falsification, or inappropriate data manipulation. The results of the present study do constitute endorsement by the American College of Sports Medicine.

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