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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.

## ABSTRACT

**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 during RUN (65.3 ml/min/kg) and XC (63.5 ml/min/kg) followed by incremental protocols at 50, 70 and 90% of speed at VO<sub>2</sub>peak 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 ( $p=.047$ ), CC ( $p<.001$ ) and PL ( $p=.031$ ) in the alpha-2 network indicated stronger modulations in network efficiency following XC. Main-effects of exercise intensity in the theta network indicated modulated SWI ( $p<.001$ ), CC ( $p<.001$ ) and PL ( $p=.003$ ) following exercise at 90% of VO<sub>2</sub>peak 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 to 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

ACCEPTED

## INTRODUCTION

Participation in endurance exercise induces acute neuroplastic changes, which result in temporary modulations-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 towards more beneficial effects at moderate and high compared to 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 due to 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 due to task-specific activation of cortical areas involved into mode-specific sensorimotor control demands (12).

Among exercise modes, cross-country (XC) skiing is unique since it requires highly developed cardiovascular capacities (16) 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 (16) make XC skiing a highly demanding full-body endurance sport. Considering the central nervous 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 (17). Depending on task constraints, the degree of activation of these sensorimotor brain areas may change due to factors such as limbs involved (18), upper and lower limb phasic coordination (19), and balance demands (20). For XC skiing, these factors differ from running (RUN), since 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. While 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 non-motor brain areas after exercise (14, 15).

To investigate changes in brain function, electroencephalography (EEG) serves as a mobile and non-invasive imaging technique with a high temporal resolution (21). Apart from EEG approaches that analyze brain function during movement that is particularly limited at high intensities due to movement artifacts, the analysis of the EEG resting states after exercise became a valid approach (22). Since 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 (RSNs), can be calculated based on temporal coherence between signals (23). RSNs are suggested to provide information on the responsiveness of the

brain to external stimuli (24) 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 (25). 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 (22). 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 a 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 (26, 27) was tested. According to previous findings, we expected exhaustive exercise to induce detrimental changes in attention-related RSNs (5, 28). With regards 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, 25). Accordingly, the findings of the present study may extend our understanding of



the neuro-regulatory effect of exercise with specific regard to exercise modes, including challenging upper and lower limb coordination (12). With regards 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 (29).

## **METHODS**

### **Participants**

We calculated a required sample size to achieve .8 statistical power at an alpha level of .05 using GPower, Version 3.1 (Faul et al., 2007), and we based assumed effect sizes on our recent publication (Büchel et al., 2021a) where we observed an effect size of .48 of exercise intensity on brain graphs in a within factors ANOVA design with two groups and 5 repetitions. This calculation led to a required participant sample size of 16. Finally, fifteen healthy young male XC skiers (20.1±.6 years, 74.4 ± 5.6 kg, 178.9 ± 5.5 cm) participated in the present investigation. Since the menstrual cycle may cause substantial day-to-day-changes in RSN organization in female participants, we preferred not to include females 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 hours per week 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 written informed consent in accordance with the Declaration of Helsinki. The study procedure 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  $\text{VO}_{2\text{peak}}$  test, ii) an XC skating  $\text{VO}_{2\text{peak}}$  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 weeks 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). Since the testing sessions needed to be fitted into the training and competition schedule of the athletes, ten athletes started with iii) and five athletes started with iv).

### Running peak oxygen uptake ( $\text{VO}_{2\text{peak}}$ ) test

The RUN  $\text{VO}_{2\text{peak}}$  test took place on a motorized treadmill (RL 2500E, Rodby, Södertälje, Sweden). To warm up, athletes performed a submaximal lactate profile starting at 8 km/h and incline of 10.5 % for 5 minutes. After each stage, a blood sample (20  $\mu\text{L}$ ) 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 km/h per stage until lactate concentration increased absolutely by 1 mmol/l compared to the previous sample and passed the 4 mmol/l threshold. After cessation of the submaximal lactate profile, participants performed an 8-minute recovery and cool-down period. The  $\text{VO}_{2\text{peak}}$  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 km/h. The test stopped at voluntary exhaustion of the participants. During the incremental test, peak oxygen uptake ( $\text{VO}_{2\text{peak}}$ ), maximum ventilation (VE), and respiratory

exchange rate (RER) were measured breath-by-breath using a stationary gas analysis system (VYNTUS CPX, Vyaire, Germany).  $\text{VO}_{2\text{peak}}$  was defined as the mean of the two highest and consecutive 30-second measurements. Accordingly,  $v\text{VO}_{2\text{peak}}$  was defined as the speed at the first of these two 30-second measurements. Simultaneously, heart rate was measured using an electrocardiogram sensor connected to a chest belt (HRM3-SS, Garmin, United States) to define peak heart rate ( $\text{HR}_{\text{peak RUN}}$ ) as the maximum heart rate reached during the RUN test. Further, a lactate sample was taken after cessation of the test.

### **XC skating peak oxygen uptake ( $\text{VO}_{2\text{peak}}$ ) test**

The XC skating  $\text{VO}_{2\text{peak}}$  test took place on an oversize motorized treadmill (RL 3500E, Rodby, Södertälje, Sweden) in the lab. All athletes were instructed to perform the skating test utilizing the skating G3 sub-technique and used the same pair of skating-roller-skis (IDT Sports, Lena, Norway) and poles adjusted for body size. Roller ski skating in the lab 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 km/h and incline of 5% for 5 minutes. After each stage, a blood sample (20  $\mu\text{L}$ ) was taken from the fingertip, and lactate concentration was analyzed. The speed was increased by 2 km/h per stage until lactate concentration increased absolutely by 1 mmol/l compared to the previous sample and passed the 4 mmol/l threshold. After cessation of the submaximal lactate profile, participants had 8 minutes to recover and cool down. The  $\text{VO}_{2\text{max}}$  test then started at 10 km/h and was performed in an incremental manner. After each minute, the speed of the treadmill was increased by 2 km/h. After reaching the speed of 20 km/h, the speed was increased by 1 km/h per minute. The test stopped at voluntary exhaustion of the participants. During the incremental skating test, peak

oxygen uptake ( $\text{VO}_{2\text{peak}}$ ), maximum ventilation (VE), and RER were measured breath by breath.  $\text{VO}_{2\text{peak}}$  was defined as the highest average of two consecutive 30-second average values. Accordingly,  $\text{vVO}_{2\text{peak}}$  was defined as the speed where athletes reached  $\text{VO}_{2\text{peak}}$ . Simultaneously, heart rate was measured to define peak heart rate skating ( $\text{HR}_{\text{peak skate}}$ ), 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  $\text{vVO}_{2\text{peak}}$ . Accordingly, the protocol consisted of four exercise stages: i) RUN/XC skating at 50%  $\text{vVO}_{2\text{peak}}$  for 10 minutes, ii) RUN/XC skating at 70%  $\text{vVO}_{2\text{peak}}$  for 10 minutes, iii) RUN/XC skating at 90%  $\text{vVO}_{2\text{peak}}$  until voluntary exhaustion, and iv) RUN/XC skating at 50%  $\text{vVO}_{2\text{peak}}$  for 8 minutes. The cool-down exercise bout was followed by 10 minutes of active recovery. If the voluntary exhaustion stage lasted longer than 5 minutes, speed was increased by 1 %  $\text{vVO}_{2\text{peak}}$  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 perceived exertion (RPE), the average and maximum heart rate during the exercise stages ( $\text{HR}_{\text{mean}}$  respectively  $\text{HR}_{\text{peak}}$ ), and during resting states ( $\text{HR}_{\text{rest mean}}$  respectively  $\text{HR}_{\text{rest peak}}$ ),

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, 25). Electrocortical activity was recorded by 65 passive wet electrodes (RNET, BrainProducts, Germany) connected to a wireless transmission system (LiveAmp, BrainProducts, Germany). 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 ~ 1.5 m ) and lasted for 5 minutes 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 minutes of recovery (REG2). An overview of the treadmill protocol is presented in Figure 1.

The fast applicability of the EEG wet electrodes allowed resting-state assessments to start within  $4 \pm 0.5$  min after stage termination of the exercise stages. Before starting the recording, electrode impedances were kept below 25 k $\Omega$  for all electrodes. Since 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, United States). Before and after applying the EEG cap, sweat

was removed from the hair and the inter-electrode 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, USA). The detailed steps of EEG preprocessing were reported in a recent article on exercise-induced changes in EEG brain graphs (25). 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/sccn/clean\\_rawdata](https://github.com/sccn/clean_rawdata)). After ASR, adaptive mixture independent component analysis (35) was applied to remove signal components from non-brain 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 (25). 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, while 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. (2021a) (5). Higher frequency bands such as beta were not considered for the present study due to reasonable day-to-day differences observed in one of our previous investigations (25).

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 inter-individual 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. Since 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  $\pm$  SD. Normal distribution of the data was verified by applying the Kolmogorov-Smirnov test. Analysis of variances (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), 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 since we observed considerable day-to-day differences, e.g., for the theta frequency band in our previous investigation (25). Since  $HR_{run}$  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  $p < .05$ . For interpretation of effect sizes, partial eta squared ( $\eta^2$ ) was calculated, and .01, .06, and .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  $HR_{rest\ mean}$  ( $F_{5,10}=56.580$ ,  $p<.001$ ,  $\eta^2=.802$ ),  $BLa$  ( $F_{5,10}=336.355$ ,  $p<.001$ ,  $\eta^2=.96$ ), and  $RPE$  ( $F_{3,12}=240.533$ ,  $p<.001$ ,  $\eta^2=.945$ ). For  $HR_{mean}$ , Friedman test also demonstrated significant main-effects of  $LOAD$  ( $Chi^2=119.806$ ,  $p<.001$ ). All outcomes demonstrated maxima after  $POST3$ . Further, Friedman test also demonstrated significant main-effects of  $MODE$  ( $Chi^2=27.74$ ,  $p<.001$ ) on  $HR_{mean}$ , with higher values for  $XC$  compared to  $RUN$ . 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  $CC$  ( $F_{4,11}=6.085$ ,  $p<.001$ ,  $\eta^2=.303$ ),  $PL$  ( $F_{4,11}=5.514$ ,  $p=.003$ ,  $\eta^2=.247$ ) and  $SWI$  ( $F_{4,11}=5.514$ ,  $p<.001$ ,  $\eta^2=.283$ ) in the theta frequency. Post-hoc analysis indicated significant lower  $CC$  and  $SWI$  at  $POST3$  compared to  $POST1$  ( $p=.049$  respectively  $p=.028$ ),  $POST2$  ( $p<.001$  respectively  $p=.002$ ), and  $REC2$  ( $p=.024$  respectively  $p=.033$ ). For  $PL$ , higher values were observed at  $POST3$  compared to  $POST1$  ( $p=.040$ ) and  $POST2$  ( $p=.004$ ).

Further, ANOVA revealed a main effect of  $MODE$  on  $CC$  ( $F_{1,14}=7.969$ ,  $p=.014$ ,  $\eta^2=.363$ ),  $PL$  ( $F_{1,14}=5.737$ ,  $p=.031$ ,  $\eta^2=.291$ ), and  $SWI$  ( $F_{1,14}=4.720$ ,  $p=.047$ ,  $\eta^2=.252$ ) in the alpha-2 frequency band. Data indicated higher  $CC$ , higher  $SWI$ , and lower  $PL$  during the  $XC$  protocol compared to  $RUN$ , 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 following 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 to RUN. For both endurance exercise modes, similar modulations of brain network efficiency appeared following exhaustive exercise load.

The main finding of the present investigation was an increased modulation of efficiency in alpha-2 networks after XC skating compared to RUN. Since 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 to 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 cortico-cortical and thalamo-cortical information flow (40). Functionally, alpha oscillations are linked to active inhibition of non-essential 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 (14), 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 due to 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 to leg activity only (18). Therefore, the active involvement of the upper body to produce propulsion during XC skiing (39) may require additional cortical resources to coordinate this movement. Further, increased information flow in the alpha-2 frequency was reported in finger movement reproductions as a function of task complexity, since more complex movements evoked stronger desynchronization in motor-related brain areas (45). Since 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 cortico-cortical information exchange after exercise cessation (14). 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 following chronic diseases such as Alzheimer's (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). Since we investigated short-term responses of the brain immediately after exercise, increased alpha-2 network modulations following XC skating compared to 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 cortico-cortical communication within the theta network may be associated with an exhaustion-induced disturbance of executive brain function (5, 28). 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). Since 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 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. (2020) extracted brain graphs from participants during graded cycling exercise and observed that facilitations of brain network efficiency appearing at moderate exercise intensity disappear when approaching heavy exercise intensity (53). Hence, our data support previous findings, which demonstrated that exercise intensity may act as a strong moderator of acute brain network responses to exercise (3, 5, 53).

### **Significance for the field**

The present findings revealed that the acute neuro-regulatory effect of exercise is modulated by two training variables: exercise intensity and mode. While intensity and duration are frequently discussed as mediators in the literature (22), only few studies have investigated exercise mode as a potential moderator of the brain's response to exercise. Our findings demonstrated that exercise with more complex demands on motor coordination might induce stronger responses in sensorimotor, task-related brain networks. During exercise modes with challenging coordination demands like XC skiing, the brain is continuously processing information, since multiple parts of the body act in concert and/ or sports specific technique becomes more complex. On a neural level, these demands may induce an additional stimulus to the brain compared to less complex exercise modes like RUN. This observation is supported by previous evidence reporting mode-specific modulations of resting-state networks applying functional magnetic resonance imaging in the context of balance and coordination training (11,

54). Therefore, exercise mode may be considered as a factor affecting exercise-induced modulations of brain networks. Considering the standardized treadmill setting the athletes were exposed to – fixed slope, speed and surface throughout the stages - one may hypothesize that the observation of mode-specific responses might become even more evoked moving lab to field conditions and increasing the variability in technique and physiological demands (55). Based on the neural efficiency hypothesis (56), it might be hypothesized that acute, exercise mode-specific modulations may result in long-term reorganization of athletes' brains when repeated consistently over time.

In the context of high-performance sports, the present findings reveal novel insights into the brain's role in exercise physiology. Future studies should indeed consider long-term adaptations of the brain to exercise. Prioritizing technique-specific endurance modalities in specific phases of the season (26) may result in chronic adaptations of the nervous system. To understand whether changes in brain communication contribute to or interfere with sports-specific performance, longitudinal investigations are required that consider both behavioral (e.g., technique) and neurophysiological (e.g., network efficiency) outcomes. Especially for exercise modes with even higher focus on sensorimotor control, brain network data may improve the understanding of differences in skill level and training adaptation (29).

### **Study Limitations**

Despite providing novel insights into the role of exercise mode on brain function, the experimental design and methodological aspects limit the generalizability of the observed findings. Notably, the investigated sample was small and consisted of highly trained male

athletes only, since fitness level, technical execution and menstrual cycle may interfere in with the results (56). However, this inclusion of highly trained individuals only limited the general availability of participants, leading to a relatively small sample size of  $n=15$ . According to the neural efficiency hypothesis (57) and explorative insights from Ludyga et al (2016), the brain's responses to exercise may vary depending on the levels of expertise (58). 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 (57), and females should be examined.

A further limitation was that the protocol order was not fully counterbalanced, since the experimental sessions were arranged according to the training schedule of the athletes. Therefore, more athletes started with RUN and less athletes (5/15) started with XC. Although the included XC athletes were familiar with the two investigated endurance modes and were regularly tested at the lab 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 (16). 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 counter-balancing and exercise familiarity should be considered as potential confounders of mode-specific modulations of brain function in athletes.

Further, 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 due to 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 (2021) suggested that particularly for intra-individual 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 to source space approaches (60). 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 artefacts contaminating the measured electrocortical potential changes. During processing, the impact of slow-drift sweating artefacts was minimized due to a high-pass filter (61) and bridged channels ( $.2 \pm 1.1$  channels/ 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 non-invasive neurophysiological methods like the EEG remain complex sources of artefact and needs 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



than an acute bout of RUN for athletes who are similarly trained in both modes. Further, 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.

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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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## FIGURE LEGENDS

**Figure 1. Overview of the experimental procedure to investigate the effect of exercise modality on brain graph modulation.** For both running (RUN) and cross-country skiing (XC), an initial incremental treadmill test on separate days allowed peak oxygen uptake ( $VO_{2peak}$ ) to be assessed. During the experimental session, electroencephalography (EEG) resting-state data, heart rate (HR), blood lactate concentration (BLa), and rate of perceived exertion using Borg Scale 6-20 (RPE) 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 speed  $VO_{2peak}$  ( $vVO_{2peak}$ ).

**Figure 2. Overview of physiological responses to different exercise loads during running (RUN, white) and cross-country skiing (XC, 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 blood lactate concentration (BLa), Subjective Rate of Perceived Exertion (RPE), Mean Heart Rate during Running ( $HR_{mean}$ ), 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, β = significantly higher than ACUTE1, # = significantly higher than ACUTE2, \* = significantly higher than ACUTE3, δ = significantly higher than REC1, § = significantly higher than REC2; level of significance =  $p < .05$ .

**Figure 3. Overview of modulations of EEG resting state clustering coefficient in response to different exercise loads during running (RUN, white) and cross-country skiing (XC, black) on the treadmill.** Modulations are displayed as % delta ( $\Delta$ ) from PRE to post-conditions regarding the calculated graph outcome in the theta ( $\theta$ , 4-8 Hz), alpha-1 ( $\alpha$ -1, 8-10.5 Hz), and alpha-2 ( $\alpha$ -2, 10-5–13 Hz) frequency bands. Post-hoc differences regarding exercise intensity are displayed as \*. Main-effects for modality are reported as †. Level of significance was set at  $p < .05$ .

**Figure 4. Overview of modulations of EEG resting state characteristic path length in response to different exercise loads during running (RUN, white) and cross-country skiing (XC, black) on the treadmill.** Modulations are displayed as % delta ( $\Delta$ ) from PRE to post-conditions regarding the calculated graph outcome in the theta ( $\theta$ , 4-8 Hz), alpha-1 ( $\alpha$ -1, 8-10.5 Hz), and alpha-2 ( $\alpha$ -2, 10-5–13 Hz) frequency bands. Post-hoc differences regarding exercise intensity are displayed as \*. Main-effects for modality are reported as †. Level of significance was set at  $p < .05$ .

**Figure 5. Overview of modulations of EEG resting state small-world index in response to different exercise loads during running (RUN, white) and cross-country skiing (XC, black) on the treadmill.** Modulations are displayed as % delta ( $\Delta$ ) from PRE to post-conditions regarding the calculated graph outcome in the theta ( $\theta$ , 4-8 Hz), alpha-1 ( $\alpha$ -1, 8-10.5 Hz), and alpha-2 ( $\alpha$ -2, 10-5–13 Hz) frequency bands. Post-hoc differences regarding exercise intensity are displayed as \*. Main-effects for modality are reported as †. Level of significance was set at  $p < .05$ .

Figure 1

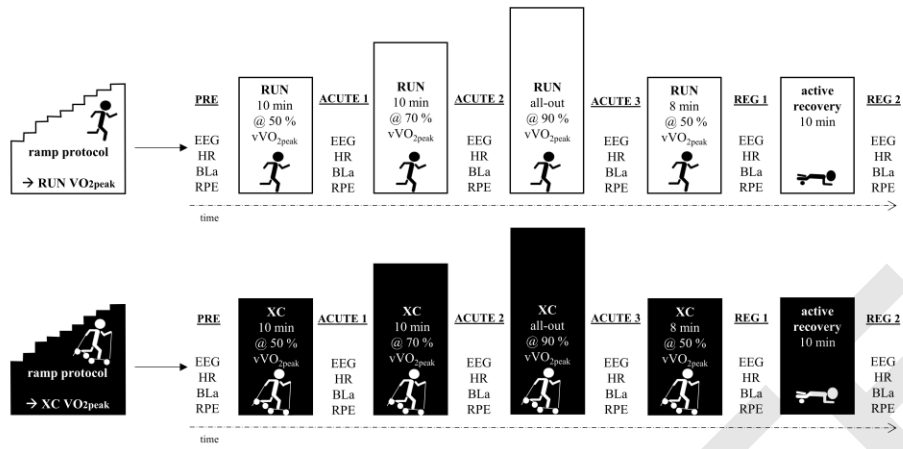


Figure 2

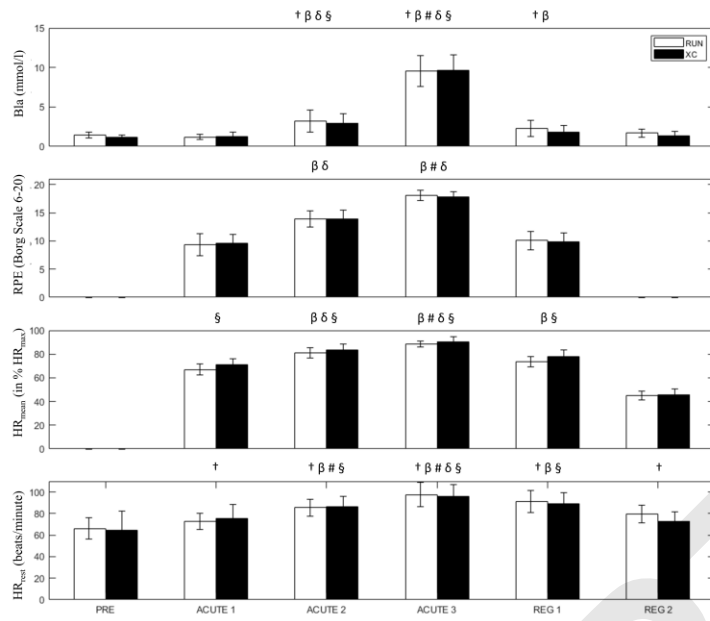


Figure 3

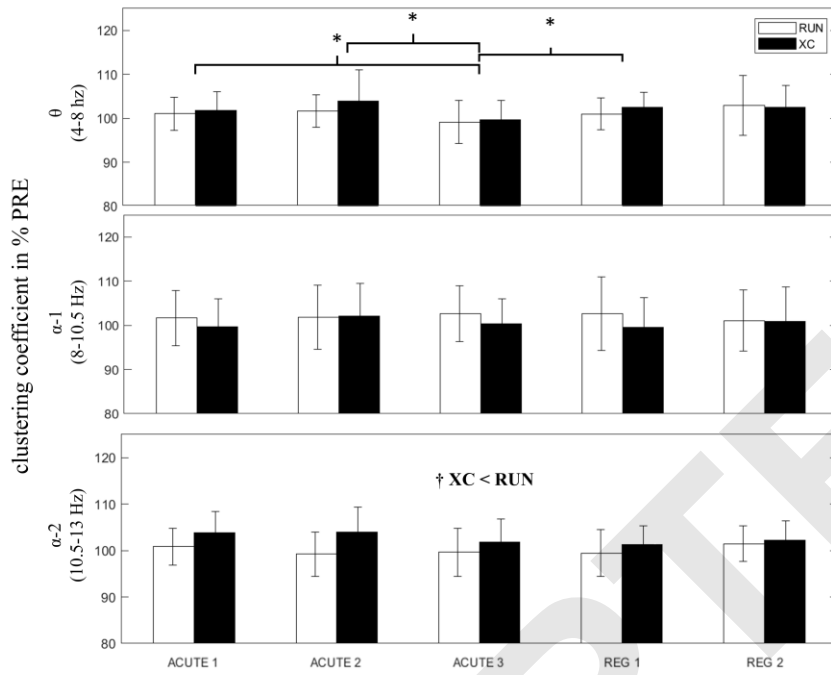


Figure 4

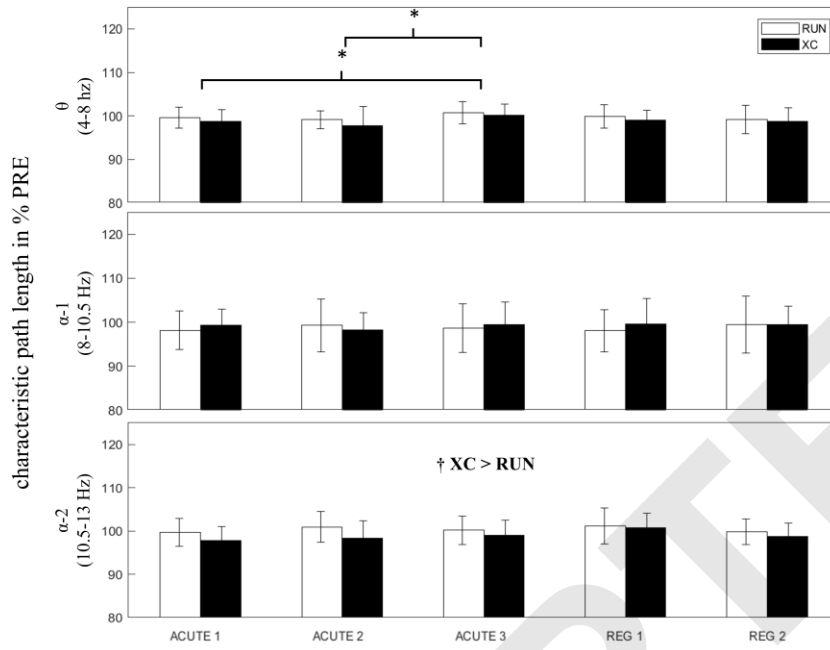
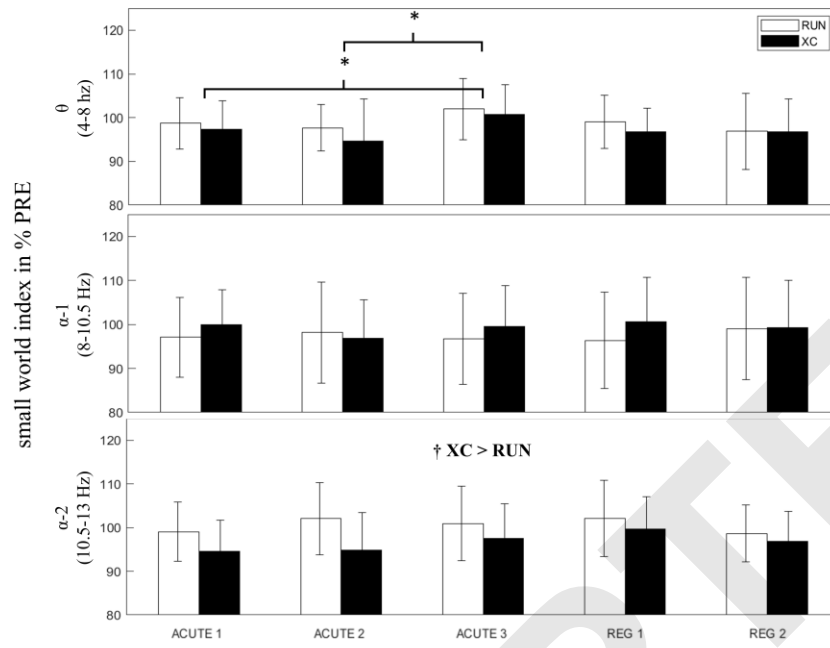




Figure 5



**Table 1. Comparison of physiological data derived from initial aerobic capacity assessment comparing running (RUN) and cross-country skiing (XC) exercise on the treadmill.**

	RUN			XC			p	r
HR <sub>peak</sub> /beats/min)	200.4	±	13.9	196.4	±	15.0	<.001	.909
VO <sub>2peak</sub> (ml/min/kg)	65.3	±	4.3	63.5	±	5.8	.015	.612
vVO <sub>2peak</sub> (km/h)	14.5	±	0.9	20.4	±	1.5	.011	.633
BLa <sub>peak</sub> /mmol/l)	11.1	±	2.0	10.5	±	2.7	.060	.496
RER (O <sub>2</sub> /CO <sub>2</sub> ratio)	1.2	±	0.4	1.1	±	0.4	.462	.206
50% vVO <sub>2peak</sub> (km/h)	6.8	±	0.4	10.2	±	0.7	.009	.648
70% vVO <sub>2peak</sub> (km/h)	9.5	±	0.5	14.3	±	1.0	.009	.648
90% vVO <sub>2peak</sub> (km/h)	12.2	±	0.7	18.4	±	1.3	.009	.648

Data assessed include peak heart rate ( $HR_{\text{peak}}$ ), peak aerobic capacity ( $VO_{2\text{peak}}$ ), speed at  $VO_{2\text{peak}}$  ( $vVO_{2\text{peak}}$ ), lactate after exercise cessation ( $BLa_{\text{peak}}$ ), and calculated speeds at 50, 70, and 90 % of  $vVO_{2\text{peak}}$ . P-values indicate the statistical differences between both protocols and r-values indicate correlation across test variables according to Pearson.

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