

How expertise changes cortical sources of EEG rhythms and functional connectivity in divers under simulated deep-sea conditions

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Abstract—Although the recent years have witnessed a growing interest in functional connectivity (FC) through brain sources, FC in extreme situations has not been completely elucidated. This study aimed at investigating whether the expertise acquired during deep-sea diving is reflected in FC in a group of professional divers (PDs) compared with a group of new divers (NDs) and how it could affect concentration and stress levels. The source of brain frequency rhythms, derived by electroencephalography (EEG) acquisition in a hyperbaric chamber, were extracted in different frequency bands and the corresponding FC was estimated in order to compare the two groups. Results highlighted a significant decrease of alpha source in PDs during air breathing and a significant increase of the upper beta source over central areas at the beginning of post-oxygen air, as well as an increase of beta FC between fronto-temporal regions in the last minutes of oxygen breathing and in the early minutes of post-oxygen air. This provides evidence in support of the hypothesis that the experience and expertise differences would modulate brain networks. These experiments provided the unique opportunity of investigating the impact of the neurophysiological activity in simulated critical scenarios in view of the investigation in real sea-water experiments.

Index Terms—EEG, hyperbaric chamber, functional connectivity, source analysis.

I. INTRODUCTION

FOR over half a century, several researchers have been investigating electroencephalographic (EEG) spectral changes associated with different brain states reflecting mental states, physiological and cognitive processes [1]. Only recently, functional connectivity (FC) has triggered the attention of the scientific community as a means for assessing brain regions interaction in mental states (e.g. anxiety, stress, and meditation) [2], disease [3], [4] or extreme situations [5].

Human brain adaptation in extreme environments is supported by the dynamic integration of neural information acquired in the new environment [6] and its non-invasive

quantification is currently a challenge for neuroscientists. To date, only a few studies have investigated FC in extreme conditions, such as simulated deep sea-environments [5], [7], altitude hypoxia [8] and microgravity [9] and, to the best of our knowledge, terrestrial extreme climatic events or conditions have not been considered so far.

This work addresses the specific case of simulation of a deep-sea environment, targeting the assessment of the EEG activity during oxygen or other gas mixtures breathing. Understanding the source of the frequency rhythms in such conditions is essential for safety as well as for the success of potential risky operations. The amount of each gas dissolved in the blood and tissues depends on the partial pressure. When this increases above a given threshold, serious disorders may occur (e.g. oxygen toxicity, nitrogen narcosis, high pressure nervous syndrome and CO₂ poisoning). The expertise of a diver results from a complex process of learning and practicing with the development of networks of implicit knowledge, technical skills, and memory [10]. EEG could be a useful tool for investigating the long-term effects induced on the central nervous system by the exposition to physical and psychological stress in underwater conditions.

EEG recordings of cerebral hypoxia have been studied since the '30s and it is well known that the electrical activity of the brain is sensitive to changes in cerebral oxygen supply [11], [12]. In awake, resting, healthy humans, a slowing of EEG activity is generally observed in investigations under the condition of acute normobaric [13], [14], [15] and hypobaric hypoxia [16], [17], [18]. In particular, EEG changes in high-altitude exposure are remarkable for an increase in delta and theta power and a decrease in alpha power [8]. On the contrary, a decrease in slow brain rhythms and an increase in fast rhythms caused by the effects of oxygen toxicity have been previously reported in a simulated deep-sea environment [5], [7] as well as in clinical practice [19]. Moreover, both increments and decrements of EEG-based FC during oxygen breathing compared to resting have been quantified in professional divers [20].

The aim of the study was to investigate whether the particular expertise acquired during deep-sea diving is reflected in brain oscillations and FC group differences in professional divers (PDs) and new divers (NDs), with respect to concentration and stress. Our hypothesis is that the acquired expertise, reflected in functional connectivity and represented in terms of EEG frequency and site, is involved in controlling visuomotor,

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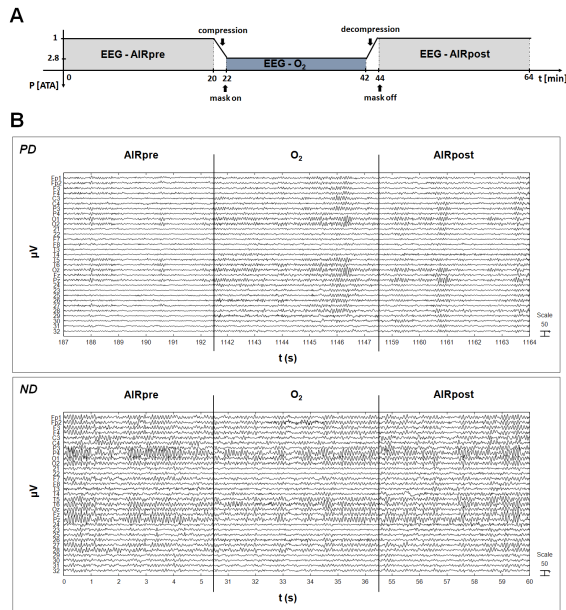


Fig. 1. (A) Dive profile. A 20-min baseline EEG recording was made at 1 ATA breathing air (EEG – AIRpre) in the open hyperbaric chamber. In the closed chamber, a 2-min compression profile (descent rate, 9 m min^{-1}) breathing air was used to reach the next stage at a pressure of 2.8 ATA (compression). At this pressure, the subject breathed pure oxygen via the oronasal mask and a 20-min EEG was acquired (EEG – O₂). After decompression, back on air breathing, the EEG of each subject was recorded for 20 min (EEG – AIRpost), discarding the first 2 min (ascent rate, 9 m min^{-1}) (decompression). (B) Example of an EEG signal after preprocessing in one PD and one ND: during air breathing (AIRpre), oxygen breathing (O₂), and air breathing after decompression (AIRpost).

spatial, and inhibitory functions. It is well known that the attentional, cognitive and emotional factors are differentially represented in terms of EEG frequency and localization. EEG alpha and theta oscillations reflect cognitive and memory performance, whereas beta band may provide a useful measure of appropriate cognitive and emotional processes [21]. In particular, theta and alpha frequency bands are associated with working memory and attention, and are altered by cognitive training [22].

In the proposed work, the linear lagged coherence was estimated at the source level as a measure of FC. Therefore, the functional brain networks, in different frequency bands, were extracted in order to compare the expert and non-expert groups. A source model (low resolution brain electromagnetic tomography (LORETA) [23]) was adopted in order to overcome limitations due to volume conduction issues [24] and to the dependence of surface potential on the EEG reference [25]. Moreover, a lagged coherence method allowed to exclude the non-lagged part of coherence [26], which includes effects of volume conduction (artificially increasing coherence). Volume conduction results in non-physiological values with zero phase lag between data time series that are annihilated by lagged coherence.

Given the importance of providing indications on the potential risk of a dive caused by oxygen toxicity we evaluated also the physiological effects of oxygen breathing on the bioelectrical activity in terms of cortical sources and brain

connectivity as compared to pre- and post-oxygen breathing in both PDs and new trainees NDs. Besides the assessment of the risk factor to which divers are exposed when operating in extreme conditions, the quantification of EEG activity in a group of non-expert subjects, could be used as a benchmark for normative data as well as for screening of candidates willing to become PDs.

II. METHODS

A. EEG data acquisition

A thirty-two channel EEG was recorded with a Bluetooth-enabled EEG system (EBNeuro – ATEs Medica Device, Verona, Italy) [5] in 22 divers (11 PDs: mean age 46.2 ± 4.9 years; 11 NDs: mean age 31.5 ± 8.9 years). A 20-min recording was carried out under three different experimental conditions, during which the subject reclined on a cot with eyes closed inside a hyperbaric chamber: air (AIRpre) (baseline at sea level, 1 atmosphere absolute pressure [ATA], in an open chamber); oxygen breathing (O₂) (at a simulated depth of 18 msw, 2.8 ATA) after 2-min of compression stage; and air (AIRpost) (after decompression, 1 ATA) (Fig.1A). For safety reasons, a technician accompanied the subjects during the dive. A closed circuit television chain, operated by the technician, was used for continuous monitoring of the process. Arousal was maintained throughout the whole recording session by administering an external acoustic stimulation as soon as one 30-s epoch showed a reduction of more than 50% of the background alpha rhythm, according to American Academy of Sleep Medicine scoring rules [27]. The procedure was supervised by an experienced neurophysiologist who was also responsible for detecting any epileptiform phenomena. The internal ethics-committee of the University of Rome, La Sapienza approved the experimental protocol and informed consent was obtained from the subjects, according to the ethical standards of the Declaration of Helsinki.

B. EEG source imaging

The data were pre-processed in Matlab (MathWorks, Natick, MA) using a dedicated home-made code and processed by a standardized low-resolution brain electromagnetic tomography toolbox (sLORETA; <http://www.unizh.ch/keyinst>, [23]) for localizing cortical sources. The EEG recordings were band-pass filtered from 1 to 30 Hz. Artifacts (i.e., eye movements, cardiac activity, and scalp muscle contraction) were visually identified and removed using independent component analysis (implemented by FastICA algorithm) and data were processed using a common average reference. The EEG data were divided into epochs of 2 s.

LORETA current density in the frequency domain can be computed from EEG cross-spectra [28]. Under the three conditions, for each subject separately and all subjects together, the EEG cross-spectra and then the corresponding 3-D-cortical distribution of the electric neuronal generators were computed with sLORETA for each frequency band, using EEG epochs of 2 s. The spectral density of estimated current density signals was mapped into a 3-D representation: one map for each frequency band in the AIRpre condition (1–20 min) and eight

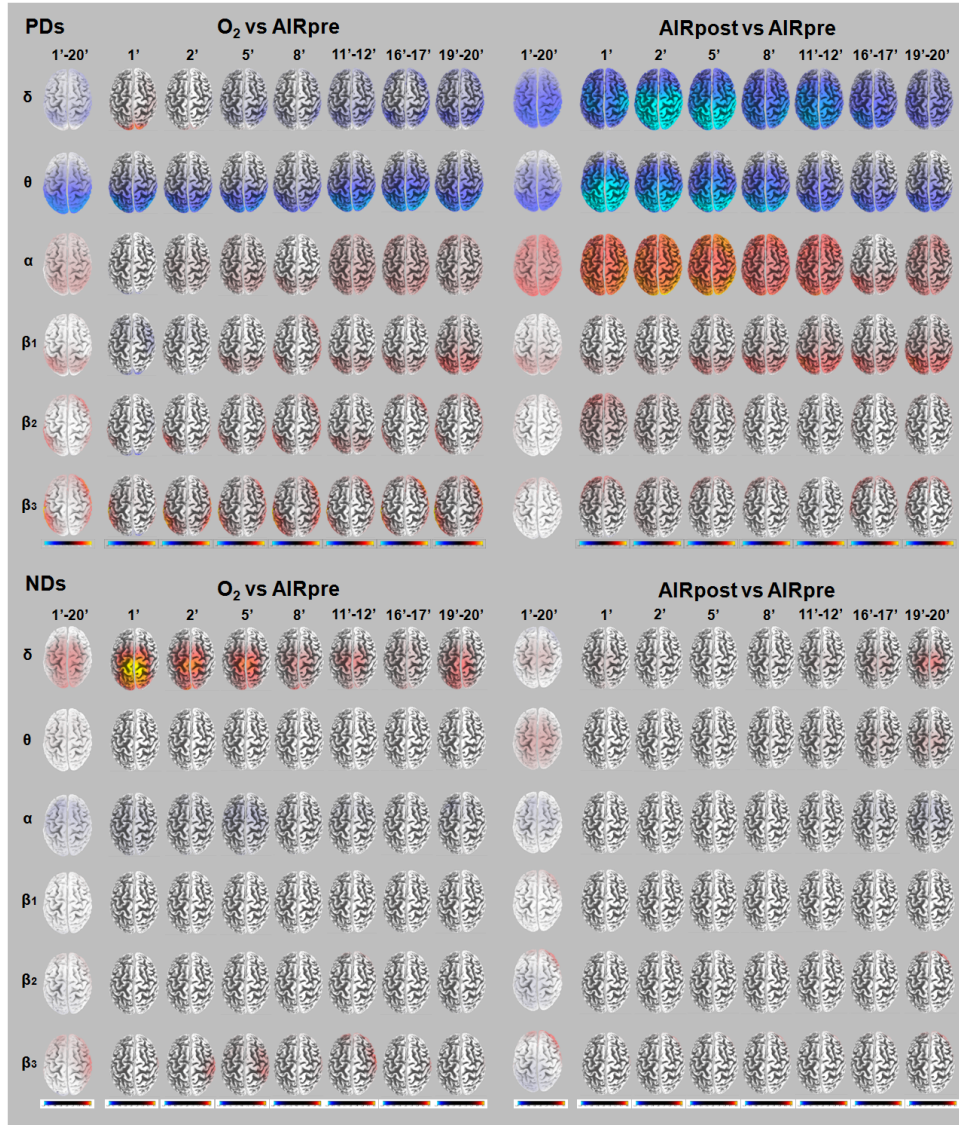


Fig. 2. Conditions comparison. sLORETA statistical maps of delta, theta, alpha, beta1, beta2, and beta3 oscillations; in PDs and NDs. Significant results are projected onto a cortical surface. Colored areas represent the spatial extent of voxels with a significant difference (yellow and light blue-coded for $p < 0.05$, corrected for multiple testing) in source in O2 versus AIRpre and AIRpost versus AIRpre. The color scale represents log F-ratio values ($p < 0.05$).

maps for the O2 and AIRpost conditions, with eight intervals of analysis (1'–20', 1', 2', 5', 8', 11'–12', 16'–17', and 19'–20'). The solution space was restricted to the cortical gray matter, corresponding to 6239 voxels (voxel size: $5 \times 5 \times 5$ mm) and the Montreal Neurologic Institute average MRI brain (MNI152) was used as a realistic head model. Statistical analyses were performed using the sLORETA software package.

The difference in source localization of EEG cross-spectra between the three experimental conditions (AIRpre, O2, AIRpost) in each frequency band was assessed by voxel-by-voxel paired sample t -tests based on sLORETA log-transformed current density power. The difference in source localization of EEG cross-spectra between the two groups was assessed by voxel-by-voxel independent sample t -tests. A non-parametric approach (statistical non-parametric mapping [SnPM]) via randomization was used (5,000 permutations) [29]. Log ratio of averages was used and the significance level was set to 0.95.

The t -values were plotted onto a magnetic resonance imaging (MRI) template with a scale bar indicating statistical power: one map for each frequency band in the AIRpre condition (minutes 1–20), and seven maps each for the O2 and AIRpost conditions, subdivided into eight intervals of analysis (1'–20', 1', 2', 5', 8', 11'–12', 16'–17', and 19'–20').

Lagged linear connectivity [26] was calculated in the same frequency ranges as follow:

$$\rho_{xy}^2(\omega) = \frac{[Im(s_{xy}(\omega))]^2}{s_{xx}(\omega)s_{yy}(\omega) - [Re(s_{xy}(\omega))]^2} \quad (1)$$

where s_{xx} and s_{yy} are the power spectral densities of two source signals x and y respectively, s_{xy} is the cross power spectral density of x and y , and ω is the reference frequency band. A whole-brain Brodmann areas (BAs) atlas was used selecting all 42 BAs in each hemisphere as regions of interests (ROIs) for connectivity analysis between the ROI centroids (single voxel). Regions of interest were sorted according to

their functional role: somatosensory, motor, executive, emotional regulation, memory, attention, sound, visual, olfactory and not well studied [30]. Connectivity contrast maps were finally calculated through multiple ROI-by-ROI comparisons using t -statistics. The significance threshold was obtained based on a permutation test with 5,000 permutations. The significant connections, corresponding to $p < 0.05$, were plotted onto a MRI template using the BrainNet Viewer toolbox [31].

Global efficiency was used as network global connectivity index. This was calculated using the brain connectivity toolbox (<https://sites.google.com/site/bctnet/Home>) as the reciprocal value of the shortest path length and is inversely related to the characteristic path length. One index for each subject and each frequency band was obtained for the three conditions. Unpaired sample t -test with Bootstrap was applied to test the differences between the two groups. Statistical significance was set at $p < 0.05$.

III. RESULTS

A. Cortical source results

Fig.1B shows the EEG signals of two representative subjects (a PD and a ND) in the three different conditions. We can qualitatively observe that the ND featured a higher amplitude EEG compared to the PD. Moreover, the EEG of the ND subject did not clearly change in the three conditions.

In figure 2 we compared the sources at each time window during O₂ and AIRpost conditions to the baseline period (AIRpre). In PDs delta and theta sources decreased in the posterior regions (Fig.2), starting from the early minutes of oxygen breathing. The alpha sources were markedly localized in the same posterior regions, albeit less significantly; whereas the beta2 and beta3 frequency bands were less involved. During AIRpost, the delta and theta sources significantly decreased from baseline (AIRpre) principally over the posterior regions until minute 5. Then, the decrease was still present but less significant over the posterior regions. The alpha and beta1 sources significantly increased in the same posterior regions during the first 2 minutes, the beta2 and beta3 frequency bands were less involved during AIRpost with respect to the baseline.

In NDs the brain source during O₂ showed a rapid increase in delta starting from the early minutes of oxygen breathing in the posterior regions (Fig.2). A decrease was observed in alpha band over central regions and an increase in beta3 over right temporal regions. During AIRpost, significant changes were observed at minutes 19–20: delta and theta source increased and alpha decreased over the central regions.

Comparing the cortical sources of PDs and NDs, some interesting observations can be made (Fig.3). During the baseline (air condition) the sources of NDs were significant greater than the sources of PDs only for the alpha frequency band and over parietal areas (in detail BA 7 and 17). Although in the last minutes of the O₂ condition and during the early minutes of AIRpost period the delta source of PDs was lower than the sources of NDs, delta, theta and alpha sources did not significantly change between groups all along the O₂ and AIRpost periods. The beta3 sources significantly increased

in PDs compared to NDs over parietal areas (BA 39, 40) at the end of O₂ and over central areas (BA 6, 24, 31) at the beginning of AIRpost. Beta1 and beta2 did not show any significant difference between groups.

B. Functional connectivity results

Figures S1-S6 display the FC between ROIs, averaged across subjects (PD first column and ND second column) in each condition; the rightmost column highlights significant FC links derived from group comparisons (see Supplementary Materials). An example for each condition and for the most significant frequency bands is illustrated in Fig.4. FC analyses revealed an increase between fronto-temporal regions representing executive and emotional regulation functions in the last minutes of oxygen breathing (11'–12' and 19'–20') and in the early and last minutes of AIRpost (1', 2', and 11'–12') in PDs compared to NDs, principally involving the upper beta frequency band. A delta FC decrease in AIRpre condition was observed in PDs compared to NDs in memory, sensorimotor and attention regions.

The FC network of the PDs demonstrated significantly higher values of beta3 global efficiency in minutes 2, 5, 8, 11–12, 16–17 and 18–20 during oxygen breathing and in minutes 1, 2, 5, 8, 11–12 in air post condition. The same pattern was observed also in beta1 (O₂: 19'–20'; AIRpost: 2', 5', 11'–12') and beta2 (AIRpost: 2', 5'). As reported also in the source analysis results, the global efficiency was greater in alpha band in NDs compared to PDs.

IV. DISCUSSION

This study targets the acquisition and processing of EEG signals during simulated under-water training of divers.

This study is the first to investigate brain functional networks in EEG recordings in PDs and NDs under simulated deep-sea conditions. Our results showed expertise-dependent differences in functional brain networks. Both source and connectivity results provided evidence of different brain oscillatory activity patterns during hyperbaric oxygen exposure highlighting different aspects of the same process.

Previous studies on brain functional networks changes during EEG recordings in PDs showed that cortical sources and connectivity patterns are affected by O₂ breathing. The O₂ condition was characterized by a marked amplitude increase of the alpha and beta sources in the parietal and occipital areas and an amplitude decrease of the delta and theta sources in the occipital area [7], with a simultaneous disconnection of the alpha and beta3 frontal-parietal links in the early minutes of O₂ breathing [20]. The main findings of this study are the boost of the alpha sources, defined as the spectral density of estimated current density signals, in NDs during AIRpre, the increase of beta sources in PDs with respect to NDs, and the beta FC increase in fronto-temporal regions in PDs at the end of O₂ breathing and during the early minutes of AIRpost.

First of all, was unexpected that during air breathing at sea level NDs showed higher alpha source compared to PDs. The neurophysiological significance of this finding contrasts with results observed by previous reports in athletes. It has

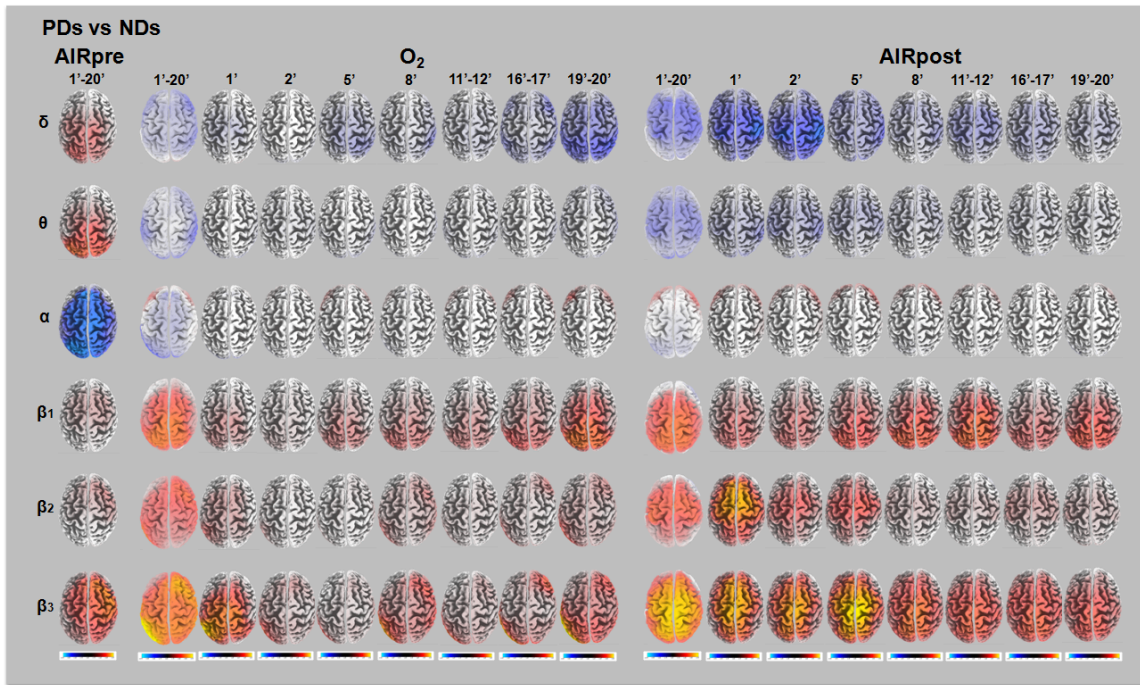


Fig. 3. Groups comparison. sLORETA statistical maps of delta, theta, alpha, beta1, beta2, and beta3 oscillations. Significant results are projected onto a cortical surface. Colored areas represent the spatial extent of voxels with a significant difference (yellow and light blue-coded for $p < 0.05$, corrected for multiple testing) in source in PDs versus NDs. The color scale represents log F-ratio values ($p < 0.05$).

been shown that professional athletes have different patterns of brain activity compared to those of beginners. The amplitude of posterior alpha sources was observed to be significantly stronger in the elite karate and gymnastic athletes than in the non-athletes or amateur athletes [32] during eyes closed resting state condition, confirming that alpha synchronization at rest is related to increased cognitive and motor performance [33]. Moreover, there is evidence that alpha power, computed at scalp level, can be increased after alpha neurofeedback training [34]. Differently, we observed stronger alpha source in non-experts. The difference in the source pattern that we found could be explained by the “neural efficiency” hypothesis [35], which suggests that experts are characterized by a more efficient cortical function in cognitive and sensorimotor tasks which results in a lower alpha synchronization. A decreased cortical activity in experts prior to a shot requiring high precision was also found in [36] and interpreted as an index for a selective event- or task-related cortical activation. Neural efficiency has also been confirmed in professional piano players, who completed a motor task with lower cortical activity than less skilled controls [37].

Another possible explanation of this behavior could be related to the effect produced by the O_2 on brain activity. In PDs, the oxygen condition and the early minutes of AIRpost, were characterized by a marked amplitude increase in the alpha sources in the parietal and occipital areas. The alpha decrease observed in group-wise analysis could be due to a “compensatory effect”. The hypothesis is that PDs are trained to breathe O_2 in extreme conditions and therefore they should be able to keep their level of alpha activity low in air condition before the experiment balancing the strong increase caused by

O_2 breathing; a sort of neural adaptation.

A second finding is that, comparing PDs and NDs, the beta3 source increased at the end of O_2 breathing and during the early minutes of AIRpost. Previous studies reported that PDs were significantly better in the cognitive processes, the act of attention, the action stability and the perception of space compared with the trainee divers [38]. Our results reported that beta3 cortical sources differed in BA 39 that is involved in cross modal association among somatosensory (body-knowledge), auditory, and visual information. In PDs this could be related to the great attention paid to the execution of the task. Beta activity is regarded as an index of information processing at the cognitive level [39] and it can increase through concentration and mental load. The high beta (beta3) is most associated with higher levels of concentration, focused attention, and arousal. Beta increases under cognitive challenge as a result of increased cortical requirements of the task. The decrease of alpha and the increase of beta power, especially in the upper range, is considered a “busy brain” [40] indicator as pointed out also by our results.

High beta brainwaves are also associated with stress and awareness. A possible explanation of beta sources increase could be related to PDs’ experience. PDs are trained to recognize stress; they learn to intervene before that stress becomes excessive and results in panic or a diving accident or fatality. However, PDs are exposed to physical and psychological stress imposed by the underwater environment and work safely. PDs involved in this study have hundreds of logged dives experience, while NDs have not enough experience to be stressed out. Moreover, PDs are aware of the task they are going to perform, the awareness that is missing in students.

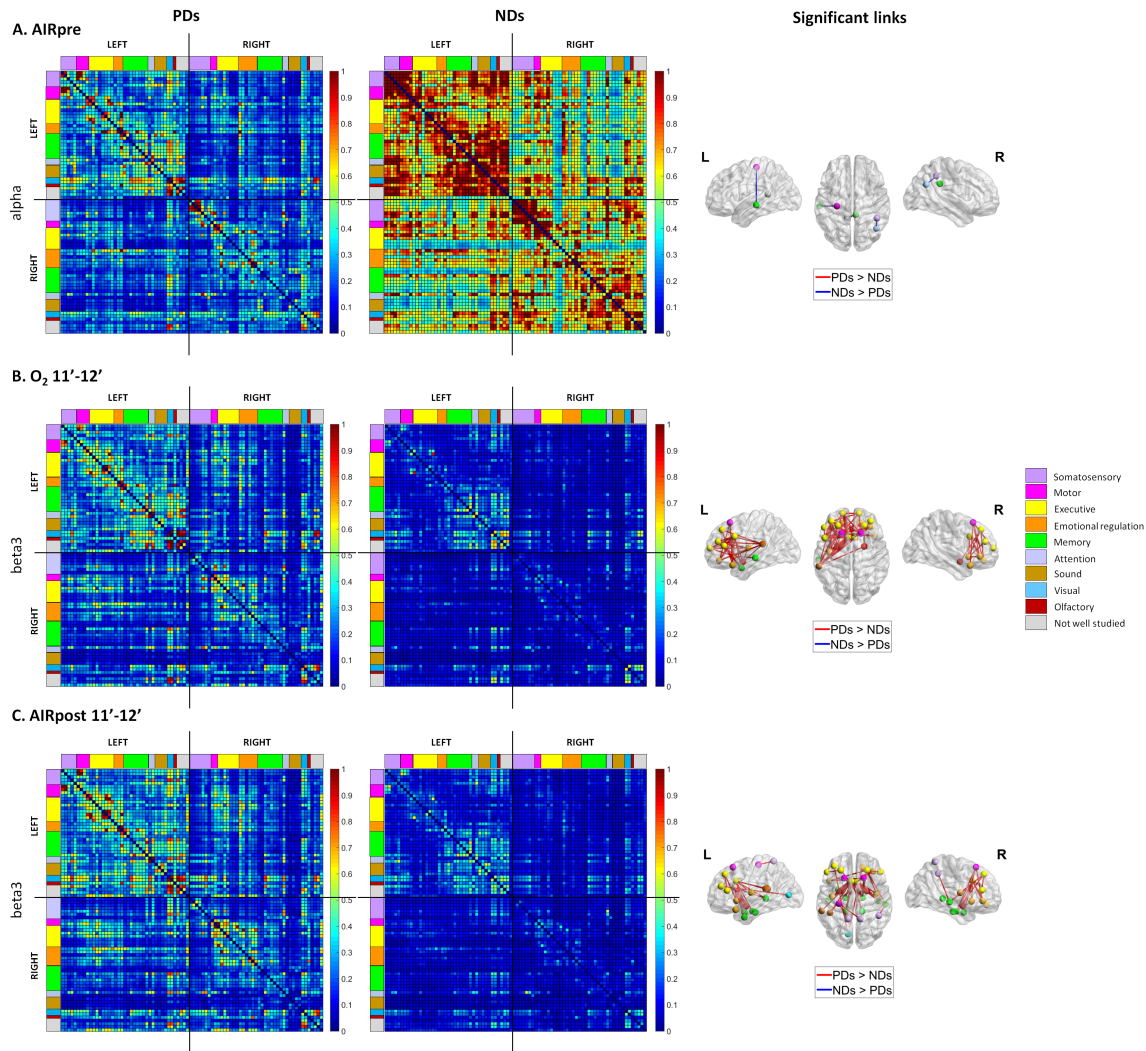


Fig. 4. Alpha functional connectivity in AIRpre (A), in O₂ (minutes 11–12) (B) and AIRpost (minutes 11–12) (C), averaged across subjects: professional divers (first column) and new divers (second column). Brodmann areas are sorted according to their functional role, represented by colors: somatosensory, motor, executive, emotional regulation, memory, attention, sound, visual, olfactory and not well studied. The third column corresponds to significant functional connectivity links derived from groups comparison ($PD > ND$: red color; $PD < ND$: blue color).

From this awareness comes also the high level of concentration and attention, demonstrated by the beta increase.

Another important finding is the strong beta FC increase between fronto-temporal regions observed in PDs compared to NDs also confirmed by the significantly higher values of beta3 global efficiency. In detail, upper beta FC changed significantly between regions designated to executive and emotional regulation functions in the last minutes of oxygen breathing and in the early and last minutes of AIRpost, when PDs showed greater FC compared to NDs. The prefrontal cortex is implicated in high-level cognitive functions, it has a prevalent role in the executive functions [41] and in emotional and motivational processes [42]. PDs are trained to plan, focus attention, remember instructions, and juggle multiple tasks successfully, differently from NDs who are at the beginning of their training.

In conclusion, our results suggest that experience and expertise differences are reflected on functional brain networks

organization. The evidence of a neural reorganization during the training opens up new perspectives in the screening and monitoring strategies of NDs. Probably, longitudinal studies will be important for a more specific characterization of brain network changes over time and for the identification of the factors associated with brain network changes during the training.

Finally, the EEG biomarkers would also provide a non-invasive tool to delineate different diving profiles providing indications on the potential risk of a dive derived from oxygen exposure. The results suggested that it may be possible to define and recognize early landmarks of oxygen-induced brain activity and FC changes in the non-expert group, compared to professional divers, highlighting a clearly different behavior with strong neurophysiological implications.

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