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Age-dependent features of EEG-reactivity—Spectral, complexity, and network characteristics

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ABSTRACT

Our goal was to measure indices characterizing EEG-reactivity in young and elderly subjects. It was hypothesized that EEG-reactivity as reflected by different measures would be lower in the elderly. In two age groups (young: $N = 23$, mean age = 21.5 ± 2.2 years; old: $N = 25$, mean age = 66.9 ± 3.6 years) absolute frequency spectra, Omega-complexity, synchronization likelihood and network properties (clustering coefficient and characteristic path length) of the EEG were analyzed in the delta, theta, alpha1, alpha2, beta1 and beta2 frequency bands occurring as a result of eyes opening. Absolute spectral power was higher in the young in the delta, alpha1 and alpha2 bands in the posterior area. The alpha1 peak frequency decreased following eyes opening in the young, while no change was observed in the elderly. Omega-complexity was higher in the elderly especially in the frontal area and increased following eyes opening. Values of the clustering coefficient, path length and that of the "small-world index" decreased as a result of eyes opening, the latter in the fast frequency range. The results suggest reduced reactivity in the elderly as shown by frequency spectra and decreased level of integrative activity particularly in the frontal area probably as a result of reduced interneuronal processing capacity. Indices of network characteristics reveal a shift towards more random topology especially in the beta frequencies caused by eyes opening.

With respect to the electrophysiological markers of physiological aging, data pertaining to the resting ("background") EEG are rather ambiguous. A moderate slowing of the alpha rhythm, a decrease of its amplitude, the increase of the theta and delta power and a shift towards generalized desynchronization have been reported but the findings are far from being consistent [11,20].

It seems reasonable to suppose that data collected during conditions in which the consequences of various types of activations and effort can be seen would be more informative on the dynamics (i.e. reactivity) of the brain, and as such, would yield valuable information on the possible changes brought about by aging. Data concerning the age-related characteristics of alpha blocking occurring in simple eyes closed–eyes open conditions are few and these indicate a reduced response in physiological aging [9]. The amplitude ratio between the EEG recorded in eyes closed and eyes open conditions declines with advancing age [13]. Alpha reactivity was found to decrease with aging in visual tasks [13,14], and mental arithmetic [14], implying a modality-independent, general phenomenon. The extent of alpha reactivity was found to be of reliable predictive value regarding cognitive performance in the elderly [27].

Linear and nonlinear analyses of EEG-complexity were also performed in the present study since these methods may be expected to reveal so far unexplored features of time-series data and are related to the degree of EEG-synchronization. Opening the eyes causes the increase of Omega-complexity [12,8]. Dimensional complexity was found to increase with aging [1]. No data are available, however, on the effect of aging on EEG-complexity with respect to reactivity.

Graph theoretical analysis was also performed on the data. In recent studies this measure proved to be a valuable index characterizing functional connectivity associated with normal [5,15,3], and pathological [16,24] brain function. This new approach allows the assessment of functional connectivity patterns and aims to specify whether or not an optimal balance between local independence and global integration can be found [26] in the system. This optimal balance was defined as one with "small-world network" characteristics in which both strong local clustering and a short characteristic path length are present [29], representing favourable conditions for information processing [23]. Smit et al. [21] found that connectivity was more random in adolescence and in old age, and was more "structured" in middle age. Micheloyannis et al. [17] concluded that the higher synchronization of fast frequencies observed in children compared to adults reflects maturational processes.

The goal of the present study was to investigate characteristic features of EEG-activation caused by eyes opening in different

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age groups. It was assumed that in the elderly following opening the eyes a reduced activation would be found due to less effective connectivity within the brain. Although changes of the alpha band are expected under these circumstances, it is not clear yet (1) if changes of other frequency bands would also be characteristic for age-dependent changes, (2) how the activation evoked by eyes opening would affect complexity- and graph-characteristics, (3) in which brain areas these would be observed, and (4) what age-dependent features would these changes show.

The data of two age groups were analyzed in this study: 18–35 years ($N = 23$; 10 women, mean age = 21.5 ± 2.2 years) and 60–75 years ($N = 25$; 19 women, mean age = 66.9 ± 3.6 years). The groups differed ($\chi^2 = 5.300$, $p = 0.021$) with respect to gender. Young adults were recruited through a part-time job agency and the elderly through advertisement and were paid for participation. The subjects had no history of any kind of neurological or psychiatric disease. According to the Hungarian version of the Wechsler Adult Intelligence Scale (MAWI) there were no significant IQ differences between the two groups (114.8 ± 11.4 and 117.8 ± 7.6 in the older and younger group, respectively; $t = 1.054$, $p = 0.062$).

The protocol was approved by the Ethics Committee of the Institute for Psychology of the Hungarian Academy of Sciences and a written informed consent was obtained from all subjects.

Electrophysiological data acquisition was performed in an electrically and acoustically shielded room. Two minute EEG-recordings were performed both in the 'eyes closed' (EC) and 'eyes open' (EO) conditions. The EEG was recorded by NuAmps amplifiers (bandpass: DC-40 Hz) (sampling rate: 1000 Hz) by Ag/AgCl electrodes placed according to the international 10/20 system, referred to the tip of the nose, with the forehead as ground. Vertical and horizontal eye movements were also recorded. The impedance of the electrodes was kept below 10 kΩ.

The offline EEG processing was performed by the NeuroScan 4.3. software, including bandpass filtering (FIR, 0.5–40 Hz, 48 dB/oct), segmentation (2048 ms long epochs), baseline correction (entire sweep) and visual artifact screening. The data obtained at the Fp1, Fp2, F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, T6, O1, O2 electrodes were analyzed. Additionally, anterior and posterior areas were studied separately.

Frequency analysis was performed by fast Fourier transform (FFT), using the NeuroScan 4.3. and Matlab 7.1 softwares in the delta (0.5–4 Hz), theta (4–8 Hz), alpha1 (8–10 Hz), alpha2 (10–12 Hz), beta1 (12–25 Hz), beta2 (25–40 Hz) frequency bands. In addition a separate analysis was performed for the alpha peak frequency in the 8–12 Hz band.

Omega-complexity, synchronization likelihood and the graph analyses were calculated by the DIGEEGXP software developed by C.J. Stam by using common average reference. Omega-complexity (OC) is a global, voltage- and frequency-independent measure, based on spatial principle component analysis performed on the covariance matrix defined by the EEG-channel data [28]. Its lowest value is 1 (maximal synchronization) and the highest value equals the number of the channels. Omega-complexity is inversely related to the average level of correlation between all the channels.

Synchronization likelihood (SL) is a measure of the degree of linear and nonlinear synchronization between two or more time series (Stam and van Dijk [25]). It is the likelihood that if a system X is in the same state at two different times i and j, then system Y will also be in the same state at times i and j. In the case of maximal synchronization this chance is 1, and for maximal independence is P_{ref}; which is a small, but non-zero number, in the present study $P_{ref} = 0.01$.

Similarly to the assessment of regional power differences, Omega-complexity and SL were either computed for all electrodes averaged over all possible pairs of EEG-channels (SL) or electrodes (Omega-complexity) yielding whole scalp results, or anterior and posterior regions.

The basic principles and formal description of graph theoretical analysis including its application to the EEG are given by Stam and Reijneveld [24] Graphs are considered to be a representation of networks which consist of a number of vertices ("nodes") and interconnecting edges characterized by their clustering coefficient (Cp) which is a measure of the local interconnectedness, and characteristic path length (Lp), which reveals its global connectivity.

Values of SL were used to construct a full matrix of all possible pair-wise combinations. This matrix was used for the calculation of the $Cp/Cp\text{-}s$ and $Lp/Lp\text{-}s$ ratios for $K = 4$, where these ratios denote values for appropriate ordered and random reference graphs (number of surrogates = 50), and K is the number of edges per vertex. "Small-world"—type organization is indicated by $Cp/Cp\text{-}s$ values being significantly higher than 1 and $Lp/Lp\text{-}s$ values being close to 1.

Statistical analyses were performed by the Statistica 8.0. software. The χ^2-test was applied for the analysis of the composition of the groups. Repeated measures of ANOVAs were performed for EEG analysis with the following factors: (1) age group (young and elderly), (2) task condition (eyes closed and eyes open), (3) frequency band (6 levels) and (4) area (anterior and posterior). When necessary, Greenhouse-Geisser correction was applied, in which cases p reflects the corrected values. Post hoc analysis was performed by using the Tukey's test, and when necessary, the Bonferroni test.

The values of all measured variables (frequency spectra, Omega-complexity, synchronization likelihood, and network characteristics) are given in Table 1.

The power of frequency spectra was lower in the elderly (group main effect: $F[1,46] = 5.841$, $p = 0.020$) and was higher in the posterior region (main area effect, $F[1,46] = 69.695$, $p < 0.001$). The area × frequency interaction ($F[5,230] = 17.609$, $p < 0.001$) showed that the delta ($p < 0.001$), alpha1 ($p < 0.001$), alpha2 ($p < 0.001$) and beta1 ($p = 0.004$) frequency bands were higher in the posterior compared to the anterior areas. An area × age group interaction ($F[1,46] = 5.623$, $p = 0.022$) was found: in both groups power was higher in the posterior than in the anterior area ($p < 0.001$); in the posterior region power was higher in the young group ($p = 0.007$). A frequency × age interaction ($F[5,230] = 4.060$, $p = 0.002$) showed that the difference between the age groups was significant in the delta ($p < 0.007$) frequency band.

The power of frequency spectra decreased after eyes opening ($F[1,46] = 36.575$, $p < 0.001$). The condition × frequency band interaction ($F[5,230] = 17.538$; $p < 0.001$) indicated that there were differences between the frequency bands: the decrease could be seen only in the alpha1 ($p < 0.001$), and alpha2 ($p < 0.001$) bands following eyes opening. A condition × area × frequency band interaction ($F[5,230] = 15.529$, $p < 0.001$) was found: in the eyes closed condition the power was higher in the posterior areas compared to the anterior areas in the delta ($p = 0.079$), alpha1 ($p < 0.001$), alpha2 ($p < 0.001$) and beta1 ($p < 0.001$) bands, while in the eyes open condition this difference was significant only for the delta band ($p = 0.032$). In the posterior region alpha1 ($p < 0.001$) and alpha2 ($p < 0.001$) power decreased after eyes opening.

A condition × age group interaction ($F[1,46] = 5.018$; $p = 0.030$, Fig. 1.) showed that the alpha peak decreased after eyes opening in the young group ($p = 0.025$), but the difference between the two groups approached zero after eyes opening.

Omega-complexity was higher in the elderly than in the young (group main effect, $F[1,46] = 4.559$, $p = 0.038$) and was higher in the anterior than in the posterior region (area main effect, $F[1,46] = 45.365$, $p < 0.001$). According to the age group × area interaction ($F[1,46] = 17.193$, $p < 0.001$, Fig. 2.) this difference was significant only for the elderly ($p < 0.001$).

Table 1
Mean and standard deviation values for the measured parameters.

	Anterior						Posterior					
	Delta	Theta	Alpha1	Alpha2	Beta1	Beta2	Delta	Theta	Alpha1	Alpha2	Beta1	Beta2
Young: power ($\mu V^2/Hz$)												
EC	46.2 ± 9.0	18.6 ± 6.6	12.4 ± 9.5	7.8 ± 5.9	14.1 ± 5.1	7.4 ± 3.7	67.7 ± 17.9	29.6 ± 19.5	85.6 ± 85.6	74.4 ± 89.1	33.7 ± 14.3	11.2 ± 7.4
EO	39.1 ± 6.9	14.5 ± 4.0	6.5 ± 8.0	3.6 ± 2.1	11.8 ± 3.7	6.9 ± 3.5	58.5 ± 14.5	17.0 ± 5.8	21.6 ± 29.2	18.0 ± 18.1	22.5 ± 11.7	10.2 ± 7.6
Elderly: power ($\mu V^2/Hz$)												
EC	33.4 ± 14.9	11.2 ± 7.1	11.0 ± 10.6	4.7 ± 3.1	15.0 ± 7.5	8.8 ± 7.8	39.6 ± 16.9	19.2 ± 17.1	67.1 ± 95.6	32.5 ± 38.4	31.9 ± 22.2	10.3 ± 8.7
EO	28.4 ± 10.4	8.3 ± 4.5	4.6 ± 3.6	3.3 ± 2.5	17.6 ± 12.0	15.1 ± 16.0	38.7 ± 13.5	12.2 ± 6.4	11.2 ± 10.9	10.3 ± 11.5	23.1 ± 12.9	10.9 ± 6.7
Young: Omega-complexity												
EC	1.98 ± 0.16	1.85 ± 0.11	1.83 ± 0.15	1.90 ± 0.15	2.18 ± 0.21	2.36 ± 0.43	1.99 ± 0.17	1.97 ± 0.16	2.09 ± 0.21	2.23 ± 0.25	2.58 ± 0.47	2.77 ± 0.67
EO	1.76 ± 0.13	2.01 ± 0.22	2.04 ± 0.30	2.07 ± 0.33	2.26 ± 0.35	2.17 ± 0.37	1.70 ± 0.15	1.90 ± 0.19	2.02 ± 0.26	2.11 ± 0.29	2.30 ± 0.40	2.21 ± 0.52
Elderly: Omega-complexity												
EC	2.17 ± 0.20	2.07 ± 0.23	2.07 ± 0.31	2.18 ± 0.34	2.42 ± 0.42	2.54 ± 0.58	2.27 ± 0.25	2.27 ± 0.23	2.48 ± 0.39	2.68 ± 0.54	3.08 ± 0.75	3.18 ± 0.90
EO	1.76 ± 0.15	1.91 ± 0.26	1.96 ± 0.27	2.00 ± 0.25	2.14 ± 0.25	2.08 ± 0.32	1.73 ± 0.15	1.87 ± 0.24	2.00 ± 0.26	2.09 ± 0.26	2.20 ± 0.28	2.06 ± 0.38
Young: synchronization likelihood												
EC	0.610 ± 0.014	0.624 ± 0.014	0.635 ± 0.020	0.633 ± 0.017	0.633 ± 0.015	0.632 ± 0.025	0.610 ± 0.013	0.610 ± 0.014	0.611 ± 0.015	0.607 ± 0.014	0.610 ± 0.021	0.608 ± 0.029
EO	0.634 ± 0.017	0.628 ± 0.020	0.635 ± 0.036	0.632 ± 0.038	0.627 ± 0.028	0.640 ± 0.029	0.644 ± 0.019	0.629 ± 0.018	0.624 ± 0.025	0.618 ± 0.024	0.622 ± 0.024	0.642 ± 0.038
Elderly: synchronization likelihood												
EC	0.599 ± 0.016	0.612 ± 0.023	0.623 ± 0.030	0.616 ± 0.025	0.620 ± 0.026	0.620 ± 0.036	0.598 ± 0.018	0.596 ± 0.014	0.593 ± 0.018	0.587 ± 0.020	0.590 ± 0.028	0.592 ± 0.040
EO	0.633 ± 0.020	0.637 ± 0.026	0.638 ± 0.032	0.631 ± 0.027	0.634 ± 0.023	0.646 ± 0.034	0.637 ± 0.018	0.631 ± 0.026	0.621 ± 0.024	0.616 ± 0.022	0.628 ± 0.025	0.652 ± 0.043

	Delta	Theta	Alpha1	Alpha2	Beta1	Beta2
Young: *Cp*/*Cp-s*						
EC	2.26 ± 0.06	2.15 ± 0.16	2.48 ± 0.15	2.47 ± 0.14	2.16 ± 0.16	1.93 ± 0.12
EO	2.26 ± 0.07	2.05 ± 0.07	2.25 ± 0.14	2.30 ± 0.14	1.95 ± 0.14	1.87 ± 0.15
Elderly: *Cp*/*Cp-s*						
EC	2.25 ± 0.08	2.09 ± 0.15	2.38 ± 0.17	2.35 ± 0.15	2.04 ± 0.19	1.92 ± 0.13
EO	2.22 ± 0.10	2.00 ± 0.09	2.16 ± 0.14	2.17 ± 0.14	1.89 ± 0.18	1.83 ± 0.17
Young: *Lp*/*Lp-s*						
EC	1.42 ± 0.03	1.40 ± 0.08	1.59 ± 0.14	1.59 ± 0.15	1.43 ± 0.08	1.34 ± 0.04
EO	1.41 ± 0.03	1.35 ± 0.03	1.44 ± 0.07	1.47 ± 0.09	1.35 ± 0.04	1.33 ± 0.05
Elderly: *Lp*/*Lp-s*						
EC	1.40 ± 0.03	1.37 ± 0.08	1.52 ± 0.14	1.50 ± 0.11	1.38 ± 0.08	1.34 ± 0.05
EO	1.39 ± 0.02	1.33 ± 0.03	1.39 ± 0.08	1.40 ± 0.08	1.32 ± 0.04	1.32 ± 0.06
Young: *C*/*L*						
EC	1.60 ± 0.04	1.54 ± 0.05	1.57 ± 0.06	1.57 ± 0.07	1.51 ± 0.07	1.44 ± 0.06
EO	1.60 ± 0.04	1.52 ± 0.03	1.57 ± 0.06	1.58 ± 0.04	1.44 ± 0.07	1.41 ± 0.08
Elderly: *C*/*L*						
EC	1.61 ± 0.05	1.53 ± 0.05	1.58 ± 0.05	1.57 ± 0.06	1.47 ± 0.08	1.43 ± 0.07
EO	1.60 ± 0.06	1.50 ± 0.07	1.55 ± 0.04	1.56 ± 0.04	1.42 ± 0.10	1.38 ± 0.08

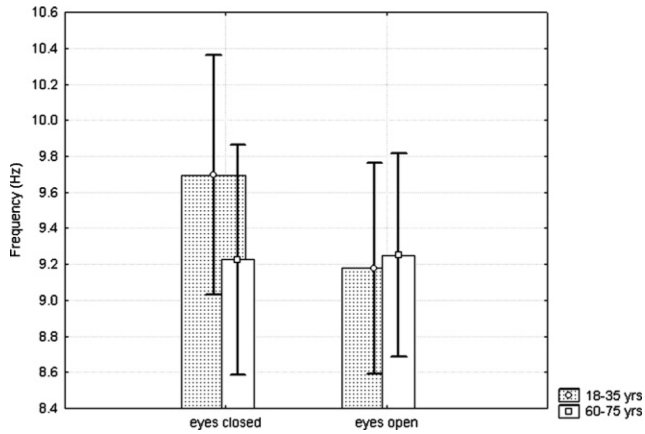

Fig. 1. Changes of the alpha peak frequency in the young and elderly subjects in the eyes open vs. eyes closed conditions. Vertical bars indicate confidence intervals.

As a result of eyes opening Omega-complexity increased (condition main effect, $F[1,46] = 44.891$, $p < 0.001$). The frequency band × condition interaction ($F[5,230] = 15.309$, $p < 0.001$) showed that this effect was significant for the alpha1, alpha2, beta1 and beta2 bands ($p < 0.001$). A condition × area × frequency band interaction ($F[5,230] = 12.248$, $p < 0.001$) was found: the increase of the Omega-complexity caused by eyes opening was significant in the theta, alpha1, alpha2, beta1 and beta2 bands only in the anterior area ($p < 0.001$, in all cases).

SL was higher in the young group (group main effect, $F[1,46] = 7.626$, $p = 0.008$) and was lower in the posterior area compared to the anterior region (area main effect, $F[1,46] = 64.063$, $p < 0.001$). An age group x area interaction ($F[1,46] = 9.471$, $p = 0.004$, Fig. 2.) was observed. Higher SL was seen in the anterior than in the posterior area in the young group ($p < 0.001$) and in the elderly ($p = 0.005$), and this measure was higher in the young than in the elderly in the anterior region ($p = 0.008$). No difference was found between the two age groups in the posterior region. The frequency × age interaction ($F[5,230] = 4.043$, $p = 0.002$) showed that SL was higher in the young group than in the elderly in the alpha2 ($p < 0.001$) band. According to the frequency × age × area interaction ($F[5,230] = 3.387$, $p = 0.006$) SL was higher in the theta ($p = 0.006$), alpha1, alpha2 and beta1 bands in the young in the anterior region compared to the posterior, while in the elderly this applied to the alpha1 and alpha2 bands ($p < 0.001$ in all cases).

SL decreased as a result of eyes opening (condition main effect, $F[1,46] = 80.315$, $p < 0.001$). According to the frequency × condition interaction ($F[5,230] = 47.390$, $p = 0.001$) the effect of eyes opening causing SL decrease was significant in the alpha1 and alpha2 ($p < 0.001$ in both) bands. SL was higher (condition × area × frequency interaction, $F[5,230] = 35.536$, $p < 0.001$) in the anterior than in the posterior region in the eyes closed condition in the alpha1, alpha2 bands ($p < 0.001$) and in the eyes open condition in the theta, alpha1, alpha2, beta1 bands ($p < 0.001$ in all cases).

The clustering coefficient (*Cp*/*Cp-s*) was lower in the elderly compared to the young group ($F[1,46] = 9.706$, $p = 0.003$). A tendency was seen for a frequency × age group interaction ($F[5,230] = 1.920$, $p = 0.092$). According to the post hoc test the difference between the groups was significant for the alpha2 frequency band ($p = 0.015$). The value of path length (*Lp*/*Lp-s*) was lower in the elderly than that seen in the young group ($F[1,46] = 7.865$, $p = 0.007$). A frequency × age group interaction ($F[5,230] = 3.022$, $p = 0.012$) was found. This difference was significant in the alpha2 frequency band ($p = 0.004$). The ratio of *Cp*/*Lp* tended to be higher in the young, but this was only a trend ($F[1,46] = 3.160$, $p = 0.082$).

Cp/*Cp-s* decreased after eyes opening ($F[1,46] = 105.460$, $p < 0.001$), which was seen in almost all bands (frequency × condition interaction, $F[5,230] = 19.985$, $p < 0.001$, post hoc: $p < 0.001$ in the theta, alpha1, alpha2 and beta1 bands, and $p = 0.002$ in the beta2 band). *Lp*/*Lp-s* decreased following eyes opening ($F[1,46] = 76.513$, $p < 0.001$). A frequency × condition interaction ($F[5,230] = 27.861$, $p < 0.001$) was observed (post hoc: theta $p < 0.001$, alpha1, alpha2, beta1 $p < 0.01$) The ratio of *Cp*/*Lp* decreased following eyes opening ($F[1,46] = 21.904$, $p < 0.001$) and a frequency × condition interaction ($F[5,230] = 4.300$, $p < 0.001$) was found: the effect of eyes opening was significant for the beta1 ($p < 0.001$) and beta2 ($p = 0.028$) frequency bands.

Given the multitude of morphological changes (shrinkage of cortical neurons, appearance of senile plaques, etc. increase of the ventricular system) along with a decrease of various neurotransmitters levels and receptors, and changes of cerebral metabolism [4,7,2] characterizing senescence—which are likely to be present to a variable degree in the elderly subjects of our study—it is to be expected that the degree of EEG-reactivity would also be reduced in the elderly [4]. It seems reasonable to suppose that the mechanisms playing a role in mediating arousal processes such as the cholinergic input from the nucleus basalis in the forebrain to the cortex [6] may also not function properly in the elderly.

A limitation of this study stems from the fact that the two age groups were unequal in terms of gender distribution. While this certainly should be considered as a suboptimal condition no consistent data are known that would suggest a convincing difference between the two sexes in terms of EEG-reactivity.

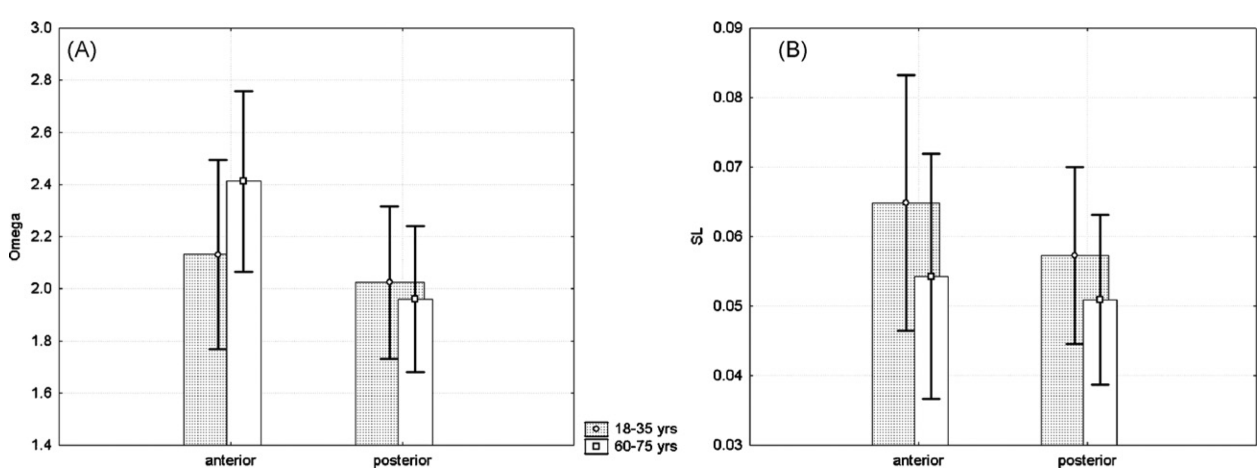

Fig. 2. Age group × area interaction for Omega-complexity (A) and for synchronization likelihood (B). Vertical bars indicate confidence intervals.

Our data do not support the notion that lower alpha frequency would characterize the EEG in old age, reported in a number of studies (reviewed by [19]). Although in the eyes closed condition a lower alpha-peak frequency was seen in the elderly, the difference between the two groups was not significant. It should also be emphasized that in the relevant studies typically the eyes closed condition was analyzed only, making direct comparison difficult. The fact that the mean age of our elderly participants was under 70 years should be taken into account.

According to our findings, the difference between the two age groups could be observed in the delta frequency band and was most apparent in the posterior area where higher power was seen in the young. The reduced absolute EEG spectral power found in the elderly is in accord with most of the earlier findings [10] although several caveats have also been pointed out by the same authors. These include methodological issues such as the use of absolute vs. relative power spectra; the possibility of enhanced inter-subject variability and others.

The higher Omega-complexity seen in the elderly probably corresponds to a reduced cooperativity within the neural elements playing part in the generation of the EEG, resulting in a decreased level of synchrony. The fact that this difference was significant for the anterior region and characterized the elderly subjects may suggest that it was caused by the changes within the frontal regions that are particularly apparent in advanced age. This possibility is supported by the observation that the synchronization likelihood was higher in the young group in the frontal area than that seen in the elderly while no differences were found between the age groups in the posterior area.

Lower values were found in the elderly for the normalized indices of both local (*Cp*/*Cp-s*) and global (*Lp*/*Lp-s*) connectedness, indicating that the brain of the elderly subjects appears to be closer to a random network. These finding support those of Smit et al. [22].

The spectral power decrease caused by eyes opening—corresponding to the well-known "desynchronization" and "alpha-blocking" phenomenon—was most apparent in the two alpha bands in the posterior region. With respect to the alpha band an obvious difference was seen between the two groups: while alpha band power decreased in the young, almost no change was observed in the elderly indicating a lack of reactivity. Thus, the intensity of the mechanisms underlying the process of activation was found to be reduced in the elderly, probably as the result of the age-related reduction of neuronal interconnectivity and less than optimal level of neurotransmission.

Increase of Omega-complexity (higher number of independent processes) and decrease of SL (reduced level of interdependencies) observed in the present study following eyes opening are findings that are in line with previous results [12,18]. While it was clear that changes of Omega-complexity elicited by eyes opening were most conspicuous in the frontal area and in the alpha and beta frequency bands, no age-related correspondence was seen. Similarly, the most conspicuous decrease of SL occurred in the alpha1 and alpha2 bands, but no age × condition interaction was observed. Thus, it appears that age-dependent characteristics with respect to the effect of eyes opening could not be verified by Omega-complexity and SL.

The reduction of values of both the path length and that of the clustering coefficient in most frequency bands caused by eyes opening may indicate a more random topology of functional brain networks, which is to be expected during desynchronization especially for path length. The value of "small-world index" (*Cp*/*Cp-s*)/(*Lp*/*Lp-s*) was found to decrease as a result of eyes opening in the beta1 and beta2 bands corresponding to a shift towards a random-like topological condition, in these frequency bands. This finding probably reflects the available capacity to react to the activation represented by opening the eyes, which appears to be unchanged in the two age groups investigated in the present study. It is to be expected that age-dependent differences in these indices would be observed if the effects of a cognitively challenging task were analyzed.

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