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Functional correlates of brain aging: beta and gamma components of event-related band responses

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The brain as a system with gradually declining resources by age maximizes its performance by neural network reorganization for greater efficiency of neuronal processes which is reflected in changes of event-related band responses (ERBRs) for sensory stimuli. Whether changes of high-frequency components of event-related responses are related to plasticity in neural recruitment during stabilization of sensory/cognitive mechanisms accompanying aging or are underlying pathological changes remains unknown.

The effect of aging on beta (β1: 12.5–20; β2: 20.5–30 Hz) and gamma (γ1: 30.5–49; γ2: 52–69 Hz) band components of ERP was studied in an auditory discrimination task (low-frequency and high-frequency tone) at frontal, central, parietal and occipital cortical locations at short latency (post-stimulus interval 0–250 ms; putative sensory processing) and long latency (250–600 ms; putative cognitive) periods.

Beta1 component of the short latency period of ERBRs was less affected by age. The beta1 activity of the long latency period was reduced by age and more widespread than in the short latency period. The aged difference in beta1 component spread into fronto-parietal regions and was more expressed after high-frequency than after low tone stimulation. Beta2 and gamma amplitudes were higher with progressive age during sensory processing. Reducing regional-process specificity with progressing age characterized tone-dependent beta2 changes during short latency (sensory), but not during long latency (cognitive) processing. Late latency (cognitive) beta2 and gamma activity diminished with age, except for the frontal high tone responses. With increasing age, gamma2 activity was more expressed over the frontal brain areas in high tone discrimination.

We concluded that age influenced more the long latency (cognitive) processes than the short latency (sensory) ones.

Key words: age effect, EEG, auditory discrimination, sensory-motor task, event-related high-frequency oscillations

INTRODUCTION

Research on aging has attracted much interest in recent years due to the increased proportion of older people in world population, with its profound implications for health care, economy, and society. Researchers differ with regard to which trends in brain activity alterations they consider most characteristic of the aging process. Age-related brain changes could lead to dedifferentiation and reduced regional-process specificity (Baltes and Lindenberger 1997), or hemispheric asymmetry reduction (Cabeza 2002) while the right hemi-aging hypothesis posits a larger decline with age in right than in left hemisphere (Rajah and D'Esposito 2005). In order to explain the increased activity in the frontal brain, Rajah and D'Esposito (2005) have suggested that functional deficit, dedifferentiation and compensation co-occur. Such a constellation of effects could be caused by atrophy in frontal brain regions or by a change in strategy caused by this atrophy (Greenwood 2007). According to the scaffolding theory of normal aging, a scaffolding process implicates the use of complementary and alternative neural circuits to achieve adaptive brain behavior during the whole lifespan, maintaining a high level of cognitive function at an advanced age (Park and Reuter-Lorenz 2009). Scaffolding as a compensatory process supposes patterns of frontal cortex overactivation with age, but may include parietal, mediotemporal and occipital regions in response to declining neural structures and function (Gutchess et al. 2005, Davis et al. 2007, Heuninckx et al. 2008). Pervasive recruitment of frontal areas, altered lateralization, and changes in the specificity of visual and auditory cortex indicate the dynamic nature of functional brain organization that can be relevant to recovery and compensatory processes across the lifespan. Research on age-related brain alterations has been conducted with electroencephalography (Goodin et al. 1978, Pfefferbaum et al. 1980, Celesia 1986, Polich 1997), magnetoencephalography (Pekkonen et al. 2005), functional magnetic resonance imaging (D'Esposito et al. 2003, Antonova et al. 2009) and positron emission spectroscopy (Cabeza et al. 1997). EEG studies have considered changes in

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brain activity mainly in the time domain. By far the most popular and classical EEG time-domain method is that of event-related potentials (ERPs). Early modal dependent and obligatory N1 and P2 components, permitting analysis of sensory events, were more pronounced with increasing age, while later N2 and P3 potentials, reflecting cognitive processes, diminished with increasing age and hemispheric asymmetry of N2 reduced with age (Dushanova and Christov 2013). Numerous age-related investigations have used not only auditory (Goodin et al. 1978, Pfefferbaum et al. 1980, Dushanova and Christov 2013), but also visual (Macpherson et al. 2009, Kukleta et al. 2010) and somatosensory (Barrett et al. 1987) stimulation paradigms. Some of these studies have yielded some common results, but others have presented contradictory findings. A previous study of age-dependent features of spontaneous EEG, using spectral power analysis, found higher delta and alpha band activity in young people than in healthy aging people (Gaál et al. 2010). Over the last decades, measurement of spontaneous EEG in normal aging has demonstrated widespread alpha power reduction, most prominent at the parietal site and stronger alpha responses only over the frontal brain region (Yordanova et al. 1998, Kolev et al. 2002). A previous study (Dushanova and Christov 2014) has also demonstrated frequency phase-locked brain oscillations delta, theta and alpha activity were more apparent with the progressive increase in age during sensory processing and age-related changes in alpha band activity focused on frontal and sensorimotor areas (Gaál et al. 2010, Dushanova and Christov 2014). Functional brain specificity diminished with increasing age and was not observed for amplitudes of low frequency (delta, theta, and alpha) oscillations during cognitive processing (Dushanova and Christov 2014). The high-frequency network was characterized by a shift towards more random topology, especially in the beta frequency band during resting state (Gaál et al. 2010). Attentional modulation with age, related to alertness deficits or vigilance deficits, was conducted with a beta-band EEG decreased activity during a simple visual attention task in elderly with low behavioral performance accuracy (Gola et al. 2012, 2013). Auditory-evoked low gamma band responses (38–40 Hz) following 40 Hz stimulation were also diminished with age in a study implementing phase-locking measures, which might be mediated by the GABAergic system (Griskova-Bulanova et al. 2013). Gamma frequency activity has been linked to a variety of perceptual and cognitive functions such as feature binding, selective attention (Engel and Singer 2001, Fell et al. 2003, Tiitinen et al. 1993, Kukleta et al. 2010). Alterations in gamma band activity have also been related to pathological processes (Llinas et al. 1999, Dushanova 2011). Spectral domain development studies have shown reduced low-frequency density and increased high-frequency density with age (Thatcher 1992, Lippe et al. 2007). Yet, results from event-related high-frequency studies still remain inconclusive as to whether changes in beta and gamma-band responses are related to plasticity in neural recruitment contributing to the stability of sensory/cognitive mechanisms accompanying aging or are underlying pathological changes. Cognitive decline and symptoms such as attention deficits, executive dysfunction, and memory impairments describe dementia in the elderly. Dementia occurs in several major neurodegenerative disorders, such as fronto-temporal dementia and hippocampal sclerosis of aging, Alzheimer's disease, and Lewy body dementia, which vary between brain regions such as the hippocampus, entorhinal cortex, medial temporal lobe, frontal cortex and inferior parietal cortex, and may explain a magnitude of deficits in different cognitive domains. Specific frequency oscillations that occur within the affected brain regions have been used to classify some idiopathic dementias as specific diseases (Dushanova 2011).

In this study, we aimed to identify the effects of aging on the specific stages of information processing in a high-frequency cortical domain (12–70 Hz). The hypothesis was that a more pronounced high-frequency pattern would correlate with sensory processing and progressive deficits in event-related high-frequency pattern processing with advancing age specifically would correlate with poorer cognitive abilities during an auditory discrimination task.

METHODS

Subjects

Forty-eight healthy volunteers participated in the study. Screening confirmed that subjects were free of past or current psychiatric and neurological disorders. All were right-handed and without deficits in hearing, clinically tested by an audiometer and based on a qualitative analysis of electrophysiological evaluation (Santos et al. 2014). Handedness was assessed by a questionnaire adapted from the Edinburgh Handedness Inventory (Oldfield 1971). Subjects were assigned to two age groups: a young group (YG, 25–31 years of age, mean age of 27 years, 13 males and 11 females) and an older group (OG, 55–60 years of age, mean age of 57 years, 13 males and 11 females). The study was approved by a research ethics committee. All subjects were thoroughly instructed about the nature of the experiment. Participants gave a written informed consent in accordance with the Declaration of Helsinki to participate in the study.

Apparatus and stimuli

Each subject was seated comfortably in an ergonomically-designed chair within an electromagnetically-shielded

Faraday cage during measurements. Subjects were acoustically stimulated binarily using two pure tones: a low-frequency tone at 800 Hz (LT), and a high-frequency tone at 1000 Hz (HT). Acoustic intensity was 60 dB. Loudspeakers were situated in front of the subjects. All measurements were executed while subjects' eyes were closed. Each experimental series consisted of 50 HT and 50 LT computer-generated acoustic stimuli with duration of 50 ms each and an inter-stimulus interval of 2.5–3.5 s, and were presented to the subject in a randomized order. The task was a binary choice-reaction sensorimotor task. Generation of motor response was a behavioral measure of aging-related slowing. While listening to acoustic stimuli, subjects reacted to a high tone by pressing a key with the left index finger, and to a low tone with the right index finger. Participants were instructed to press the key as quickly as possible with their correct index finger, so speed and accuracy had equal importance. Electroencephalography (EEG) was recorded with a Nihon Kohden EEG–4314F (cutoff frequencies of 0.3–70 Hz) using 12 Ag/AgCl electrodes attached to the subject's scalp, according to the international 10–20 system: F3, C3, P3, T3; Fz, Cz, Pz, Oz; F4, C4, P4, T4. Simultaneously, hand movement performance was tracked by means of a force profile and a surface electromyographic activity pattern (EMG) of first dorsal interosseus muscles (bandpass filtered 0.03–500 Hz). EEG records were controlled for EMG artifacts. EEG signals were referenced to both processi mastoidei and a ground electrode placed on the forehead. Records were synchronized to stimulus onset. An oculogram (EOG) was recorded from electrodes placed above and below the lateral canthus of left eye for the detection of eye movements and blink artifacts. Only artifact-free EEG records were processed. The skin impedance was controlled to be less than 4 kΩ. A second-order Notch filter was applied in order to discard the 50 Hz AC noise component, using the built-in MATLAB function. The EEG signals were digitized on-line with a sampling frequency of 500 Hz.

Reaction times were determined from force-time curves. Pressing with the index finger produced a negative deflection in the force records. The criterion for detection of the reaction onset was a drop of the force curve of more than 10% below a baseline, defined as the first 40 ms after stimulus offset. Performance accuracy was calculated by the percentage of correct responses based on 50 trials for each subject and averaged across the subjects for each stimulus.

Procedure

Repeatable signals with at least a biphasic waveform component within 1.5 s window with similar shape were termed as averaged event-related "waveforms" (ERWs) (Dushanova and Christov 2013). The parameters of the waves were computed relative to the corrected baseline, based on a 300 ms pre-stimulus period. The signals were later verified to have signal-to-noise ratio (SNR) above mean 1.1. SNRs were calculated using the following formula: SNR=A/(2*SDnoise), where the amplitude A was the peak-to-peak voltage of the mean ERW and SDnoise was the standard deviation of the noise. The noise ε was obtained by subtracting the mean from each individual averaged event-related wave (AERW). In other words, for a given single electrode, ε was the collection of residuals when the mean AERW was subtracted from each individual ERW, and SDnoise was the standard deviation over this collection. Only those single trials satisfying the rejection criterion after noise removal were included in the time-frequency analysis. The time-frequency analysis represented the time-resolved amplitude spectra of the recorded EEG signals and performed within the MATLAB software. For this purpose, the signals were processed using the fast Fourier transform algorithm with 200 ms-long sliding Hamming window and a step size of 10 ms. The average spectrograms were calculated from the single trial spectrograms. For each tone condition, the average spectrogram was used to calculate the baseline for each frequency bin. The relative single trial spectrograms were absolute single-trials spectrograms divided by each time-frequency bin relative to the baseline corresponding to this frequency bin. The calculation was done for each tone-condition separately. Relative single-trial band power amplitude modulation was investigated in four frequency sub-bands: beta1 (β1) – [12.5, 20] Hz; beta2 (β2) – [20.5, 30] Hz; gamma1 (γ1) – [30.5, 49] Hz; gamma2 (γ2) – [52, 69] Hz. The amplitude modulation in time for each of the frequency bands was the averaged amplitude across all bins in a corresponding frequency range. Activity in each frequency band was examined during the sensory processing time (T1), according to the interval of an appearance of the sensory components (N1, P2) of event-related potentials and during cognitive processing (T2), according to the time interval of an appearance of the cognitive components (N2, P3) (Dushanova and Christov 2013). Relatively, sensory processing took place during the first post-stimulus interval (T1: 0–250 ms) and cognitive processing during the second post-stimulus interval (T2: 250–600 ms) (Dushanova and Christov 2013).

Statistics

The statistical analyzes of the amplitudes of each brain frequency component (β1, β2, γ1, γ2) were performed for the post-stimulus interval and the statistical difference between the groups was assessed for each tone type by means of a bootstrap nonparametric procedure (Mason and Newton 1990). The characteristics were grouped by tone and by young and older healthy controls, and analyzed by means of a permutation test for multiple comparisons between time points for time course analysis.

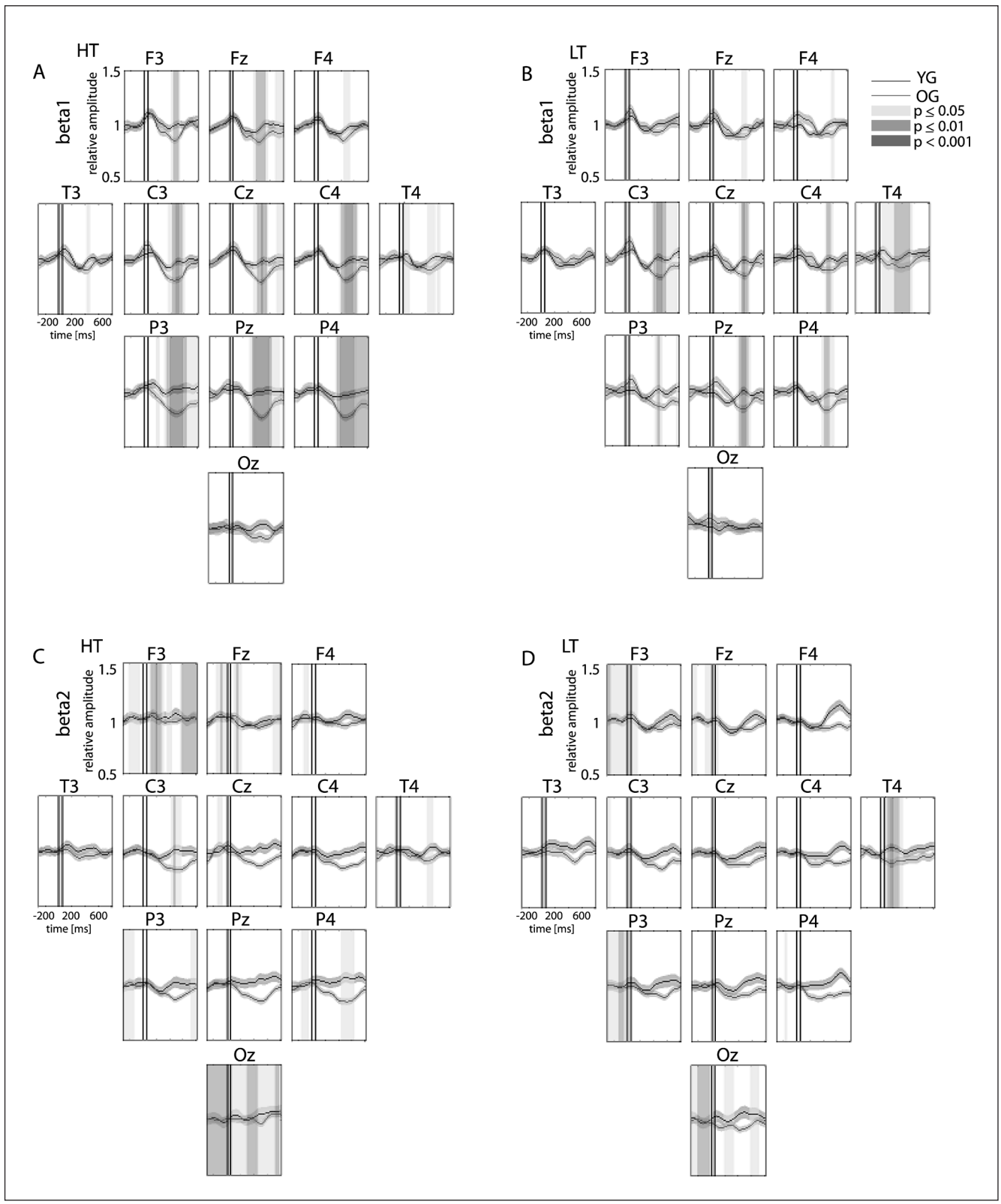

Fig. 1. Scalp distributions and statistical comparisons of the amplitudes of beta frequency band modulations for the groups (YG – black and OG – gray) during sensory-motor task for beta1 frequency band (A) HT and (B) LT; beta2 frequency band (C) HT and (D) LT. The vertical bars represent 95% confidence error bars. The colors correspond to different critical values of significance (dark gray – $p<0.001$, gray – $p<0.01$, light gray – $p<0.05$) analyzed by means of a permutation test for multiple comparisons at each time point for pairs comparison of scalp leads between young and older groups (KW test).

The computed random distribution was analyzed with a nonparametric test, i.e., Kruskal-Wallis test (P<0.05) for pairs comparison of the scalp leads between young and older groups. This procedure should reduce the influence of any random variations in experimental conditions between trials.

Reaction times and performance accuracy were compared between groups and tone condition by Kruskal--Wallis nonparametric test ([KW test], P<0.05).

RESULTS

Behavioral analysis

The right hand reaction time was significantly shorter than the left hand reaction time in OG (left hand 467.51±7.96 ms; right hand 446.54±7.80 ms; $F_{1,828}$=17.19, P=0.0475), but not significantly for YG (left hand 422.56±7.82 ms; right hand 439.10±8.55 ms, $F_{1,830}$=0.19, P=0.24). In between-group comparison YG presented faster reactions, but significantly only for the left hand (YG 422.56±7.82 ms; OG 467.51±7.96 ms; $F_{1,830}$=32.87, P<0.001), not for the right hand (YG 439.10±8.55 ms; OG 446.54±7.80 ms; $F_{1,830}$=0.11, P<0.099).

Although the performance accuracy of the sensory-motor task tended to be slightly greater at high-frequency tone stimulation in each group (mean ±SE, YG 99.3%±0.7, OG 98.82%±1.18; $F_{1,830}$=0.0006, P=0.98), in comparison with the accuracy at low-frequency tone stimulation, (mean ±SE, YG 98.7%±1.66, OG 97.17%±1.36; $F_{1,830}$=0.008, P=0.7), there were no significant differences in accuracy across conditions and groups.

Between-group differences in brain oscillation components during sensory processing

Scalp distributions of patterns of average time-frequency amplitude changes overall YG and OG trials are shown in response to HT (Figs 1, 2A, 2C) and LT (Figs 1, 2B, 2D).

During sensory processing (T1: 50–250 ms):

1) β1 amplitude was significantly lower for OG compared to YG over the right temporal area only, either tone, (T4: $F_{1,828}$>15.3, P<0.05, KW test; Fig. 1A, 1B);

2) β1 amplitude appeared earlier with a shorter duration in OG than in YG over the right temporal area only, earlier after HT than LT;

3) significantly lower β1 amplitude was observed at the left parietal area after HT only ($F_{1,828}$=10.4, P<0.05; Fig. 1B).

For either tone, the β2 amplitude was significantly higher at central and left frontal areas in OG than in YG (HT: $F_{1,830}$>25.3, P<0.01, Fig. 1A; LT: $F_{1,828}$>13.3, P<0.05, Fig. 1B). The duration of β2 amplitude difference between groups was longer after HT than LT. The β2 activity was significantly lower in OG over the right temporal side for LT ($F_{1,828}$>19.1, P<0.01 for time interval 50–250 ms, Fig. 1B) and over the occipital side for either tone ($F_{1,828}$>13.1, P<0.05).

Higher γ1 activity was found in YG after LT and in OG after HT during the first 100 ms after stimulus onset at central, parietal and occipital electrodes (HT: Cz, P<0.01; C4, P<0.05; P3, Pz, P4, Oz, P<0.001; Fig. 2A; LT: Cz, P<0.05; P3, Oz, P<0.001; Pz, C4, P4, P<0.01, Fig. 2B). An opposite γ1 amplitude relationship was observed between groups at frontal areas during the first 100 ms:

1) significantly higher γ1 for YG after HT and for OG after LT at the fronto-central side;

2) higher γ1 for YG at the left frontal area and for OG at the right frontal area after both tones (HT: F3, P<0.01; Fz, F4, P<0.05; Fig. 2A; LT: F3, P<0.05; Fz, F4, P<0.01; Fig. 2B).

Higher γ1 activity was found in OG than in YG during the next 100 ms after stimulus onset at the frontal areas, either tone (HT: F3, P<0.001; Fz, F4, P<0.01; Fig. 2A; LT: F3, F4, P<0.05; Fz, P<0.01; Fig. 2B; except F3 after LT, where $\gamma1_{OG}<\gamma1_{YG}$).

OG demonstrated significantly higher γ2 amplitude than YG after stimulus onset of HT during the early post-stimulus interval (100–300 ms) overall for frontal areas, vertex, right sensorimotor, and parietal leads (F3, P3, Pz, P<0.001; Fz, F4, C4, P<0.01; Cz, P<0.05; Fig. 2C). Higher γ2 OG amplitude was observed in right fronto-parietal areas, vertex and central parietal-occipital sides after LT (F4, Cz, P<0.05; Pz, Oz, P<0.001; P4, P<0.01; Fig. 2D). Higher γ2 was found for YG at lateral parietal areas and central occipital lead after HT (P3, P4, P<0.01; Oz, P<0.001; Fig. 2C) and at the left fronto-parietal side after LT (F3, P<0.01; P3, P<0.001; Fig. 2D).

Between-group differences in brain oscillation components during cognitive processing

OG showed significantly lower whole-brain β1 during cognitive processing for either tone (400–600 ms, Fig. 1A, B; except Oz, either tone, F3 and T3 by LT stimulation). Between-group difference increased in fronto-parietal direction more expressed after HT ($F_{1,830}$>28.7, P<0.001 for more of the channels Fig. 1A), and started earlier with a prolonged duration after HT than after LT ($F_{1,628}$>19.1, P<0.01 for more of the channels, Fig. 1B).

A lower β2-amplitude was observed in OG than in YG during cognitive processing (250–600 ms), although significant change occurred only at F3, C3, P4, T4 and Oz after HT (P<0.05, Fig. 1A).

Significantly lower γ1 activity was found in OG during cognitive processing at the vertex (after 250 ms), parietal areas, centro-occipital side after HT (Cz, P<0.05; P3, Pz, P4, P<0.01; Oz, P<0.001), at F3, P3 and Pz electrodes

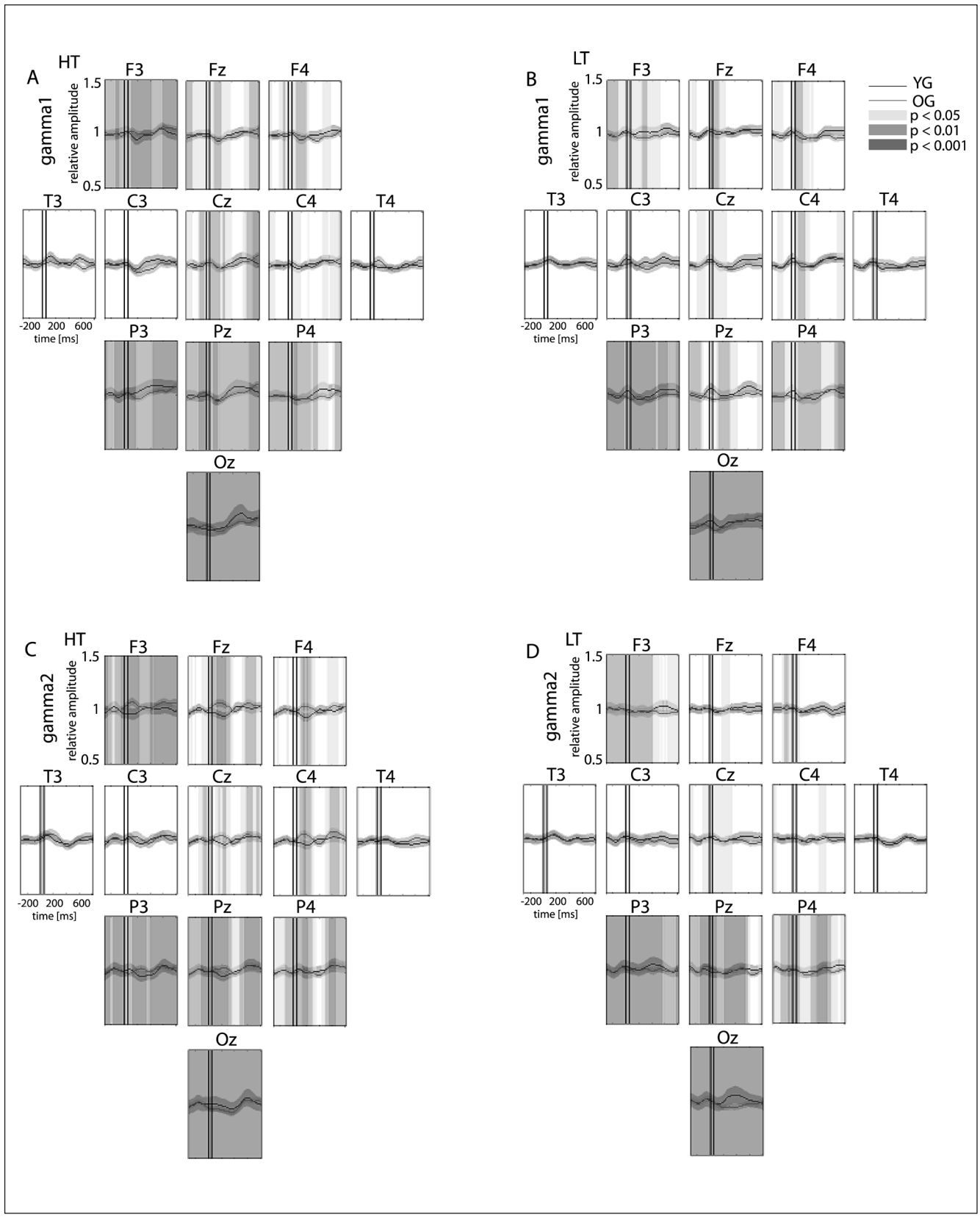

Fig. 2. Scalp distributions and statistical comparisons of the amplitudes of gamma frequency band modulations for both tones (YG – black and YG – gray): gamma1 frequency band (A) HT and (B) LT; gamma2 frequency band (C), HT and (D) LT. The format is the same as Fig. 1.

after LT (F3, Pz, P<0.05; P3, P<0.001). On the other hand, γ1-amplitudes in OG significantly exceeded those in YG between 700 and 800 ms after HT at the head-midline electrodes (Fz, Cz, Pz, P<0.001) and after LT only at P4 (P<0.001).

The γ2 was significantly increased for OG as compared to YG after HT during the late post-stimulus interval (500-700 ms) at frontal and central electrodes (F3, P<0.001; Fz, Cz, C4, P<0.01; F4, P<0.05; Fig. 2C).

Within-group differences in brain oscillations between tone stimulation

YG did not show a significant difference in high--frequency oscillation activity with regard to the tones.

Higher β1 was found only for OG after LT during cognitive processing at right sensorimotor (400–500 ms; $F_{1,830}$>14.7, P<0.05), left temporal areas (400–425 ms; $F_{1,830}$>13.4, P<0.05), and later at fronto-central side (700–800 ms; $F_{1,830}$>16.4, P<0.05; Fig. 3A).

OG demonstrated a significant difference in β2 frequency band with regard to the tone types (Fig. 3B). β2 amplitude was higher after HT at left frontal (200–300 ms; 500–525 ms; $F_{1,830}$>14.2, P<0.05) and centro-occipital leads (380–410 ms; 750–800 ms; $F_{1,830}$>12.0, P<0.05). Opposite amplitude relation, higher β2 amplitude after LT than after HT, was observed at right sensorimotor (475–500 ms; $F_{1,830}$>14.1, P<0.05), centro-parietal (490–570 ms; $F_{1,830}$>15.6, P<0.05) and right parietal leads (435–580 ms; $F_{1,830}$>16.2, P<0.05; Fig. 3B).

OG γ1 was significantly higher after HT than after LT at the vertex (690–800 ms, $F_{1,830}$>15.6, P<0.05) and centro-parietal area (630–800 ms, $F_{1,830}$>19.8, P<0.01; Fig. 3C).

Within-OG group tone-stimulation differences in γ2 activity were observed only frontally with significantly higher γ2 amplitude after HT than after LT during sensory processing (F3, Fz, F4; $F_{1,830}$>11.5, P<0.05). A significantly more prevalent γ2 amplitude was found in OG after HT at head-midline electrodes (Fz, Cz, Pz, Oz; $F_{1,830}$>14.6, P<0.05), right-hemisphere (F4, C4, P4, $F_{1,830}$>13.8, P<0.05) and left frontal side during cognitive processing ($F_{1,830}$=19.8, P<0.01; Fig. 3D).

DISCUSSION

The obtained results confirmed that event-related oscillatory responses in different high-frequency bands modulate with age during sensory and cognitive processes. Functional differences were found between high-frequency event-related oscillatory activity in sensory-motor information processing of elderly group and young group in both stimulus encoding and cognitive processing.

More pronounced Beta2 and gamma activity with progressive age during sensory processing

Beta activity has been shown to be correlated with attention and perception (Farmer 1998, Kopell et al. 2000, Gola et al. 2012, 2013), and also with the long-range synchronous activity of neocortical regions (Roelfsema et al. 1997). Thus, the lower β1-activity in the elderly group than in the young group during the sensory processing of high tone stimulation might reflect an attentional shift towards the high-frequency acoustic stimuli. The early appearance of a β2 between-group difference may be linked to the early lower gamma oscillations (Roelfsema et al. 1997, Pantev 1995). This early aged β2 difference could be explained by different levels of processes such as attention or stimulus perception. Short-term intervals of significant between-groups γ1 and γ2 differences were found across the tones. During the stimulus duration, significantly more prominent γ1 activity appeared at right/left frontal area for elderly/young group after either tone, but only the elderly group showed short-term higher γ1 burst at stimulus offset over the frontal areas after either tone and the young group γ1 activity was more pronounced (than for the elderly group) at the other brain areas depending on tone type. The primary neural source of the early gamma oscillations (around 40 Hz) has found in the auditory cortex (Pantev et al. 1991). The early γ1 modulations reflect an essential component in perceptual processing (Pantev et al. 1991) or phase-locked sensory phenomenon (Karakas and Basar 1998), prone to different attention levels, important for preparing the brain for subsequent processing (Tallon-Baudry and Bertrand 1999, Dushanova 2011). The task complexity may enhance most considerably the sensory processing in the frontal areas because of increased attention level. Hence, the ability of attention level modulation in γ1 band seen for the young group during early sensory processing in other cortical areas may diminish or disappear with increasing age.

The binary motor task produced widespread and lasting between-group differences in γ2 activity. With increasing age, the parietal areas become sensitive earlier (i.e., with an earlier γ2 difference) to immediate auditory stimulation irrespective of tone frequency, perhaps due to higher arousal state (Pulvermüller et al. 1997). During the high tone stimulus duration, γ2 activity was more exaggerated in the elderly group over anterior brain areas and at posterior brain areas in the young group, while during the low-tone stimulus duration γ2 activity was increased at right fronto-parietal and central parietal-occipital sides for the elderly group, and at left frontal and parietal areas for the young group. The centers of very early sensory processing when a motor reaction was involved might switch from posterior to anterior brain regions with advancing age.

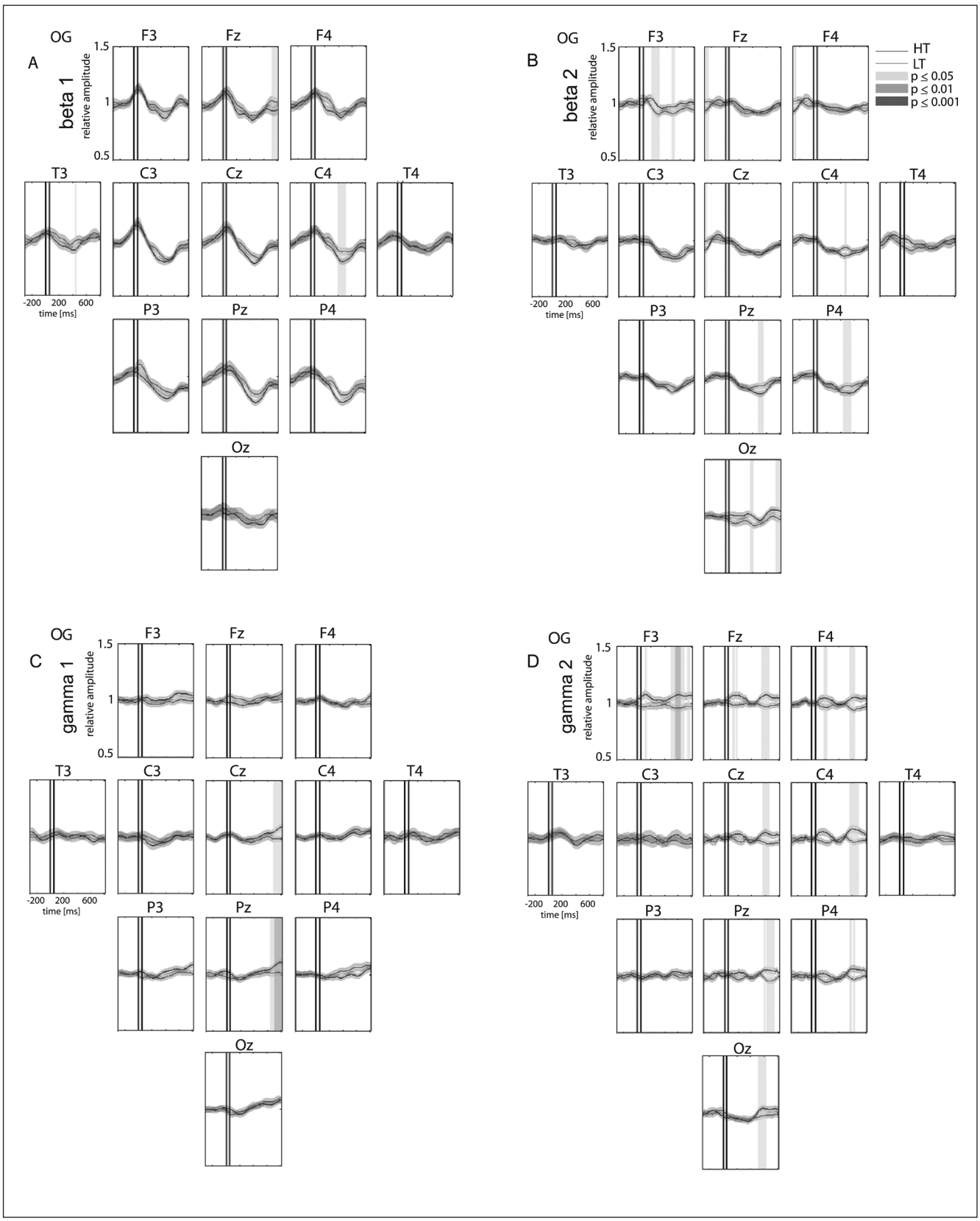

Fig. 3. Scalp distributions and statistical comparisons of the amplitudes of the frequency band modulations for OG (HT – black and LT – gray): (A) beta1 and (B) beta2 frequency band; (C) gamma1 and (D) gamma2 frequency band. The format is the same as Fig. 1.

The age reduced the cognitive processes

The elderly β1 activity was significantly lower than for the young group at all leads during cognitive processing. The between-group β1 difference increased in fronto-parietal direction was more expressed after a high-frequency tone than after low-frequency tone stimulation. The beta rebound effect was the greatest between-group difference, present at the contralateral sensorimotor areas. The early elderly lower β1 activity was a result from an attentional shift towards the movement task at the expense of the high tone perception. The later detected significant between-group difference demonstrated that brain processes, leading to cognitive β1 changes in the elderly group, lagged as compared to the young group. This observation could be accounted for by different temporal event-related desynchronization effects due to cognitive processes or by motor imagery in response to the non-adequate tone stimulus (Neuper and Pfurtscheller 1999). Over the sensorimotor areas, event-related desynchronization (ERD) and a later rebound event-related synchronization (ERS) in the beta frequency range (14–35 Hz) have been found to relate to movement execution (Stancák and Pfurstcheller 1996). Thus, the observed differences in β1 oscillations between the groups in the central brain areas might reflect stronger β1-ERD effect on the adult subjects when the movement was involved. Beta frequency responses (mainly ERD) have also been associated with an auditory memory (Karrasch et al. 2004, Pesonen et al. 2006), cognitive control of behavior or "executive functions" (Pfurtscheller and Lopes da Silva 1999, Engel et al. 2001). Some investigations (Sutoh et al. 2000, Basar et al. 2001, Gurtubay et al. 2001) propose beta and gamma cortical rhythms may serve cognitive processes such as linking perception to action or being involved in movement planning (Donoghue et al. 1998). By investigating the effects of normal aging, Karrasch et al. (2004) even found young and older groups performed equally well behaviorally, but they have seen aging effects in oscillatory beta responses, especially during working memory retrieval in 400–700 ms period, at central and right temporal regions. They further noted memory-related brain processes are the first affected in older age. The lower β1 activity observed for the elderly group during cognitive processing might be explained by enhanced ERD due to changes in the cognitive processes. Close to the task end, greater β1 decrease in the elderly group than in the young group was most probably caused by stronger movement-related effect, whereby increasing age may lead to a more widespread expression of this effect. Late post-stimulus frontal β1 increase was evident only in the young group following high tone stimulation (non-dominant left-hand movement), which may represent an inhibited frontal cortical network, at least as noted under certain circumstances (Pfurtscheller and Lopes da Silva 1999, Engel et al. 2001).

The groups manifested opposite β2 amplitude relations during the sensory and cognitive stage. Significantly more pronounced OG β2 decrease was elicited over the anterior left hemisphere and posterior right hemisphere after high-frequency tone stimulation, which may be explained by higher attention or arousal levels with respect to the high tone stimulation. Late β2 and β1 age-related decrease could be a result of higher levels of movement-related desynchronization or different motor-related cognitive behavior as high attentional level after high-tone stimulation. High-frequency beta sub-bands in voluntary motor control relate to initiation of movement, i.e., ERD in the 20–30 Hz band while ERS in low-frequency beta sub-bands (12–16 Hz) relate to the stopping of planned action (Pfurtscheller and Lopes da Silva 1999, Engel et al. 2001). Therefore, low-frequency beta sub-bands represented inhibitory components of cognitive control and were more generalized, while higher frequency beta sub-bands took part in response choice and were more specialized in terms of both function and cortical distribution. The β2 decrease during the early cognitive period may reflect cognitive ERD related to tone type discrimination and a suppression of hand movement in response to low tone type. The cognitive β2-ERD, more prominent by movements made with the left hand, becomes more evident with progressing age. Close to task end, elderly β2 increased significantly (more than in the young group) at the central and left frontal areas after high tone stimulation, but not after low-frequency tone stimulation. Thus, the groups may apply different cognitive strategies for high tone discrimination (non-dominant reaction) and could be related to late inhibited frontal cortical networks after movement execution. Information processing of movement-related behavior predominantly engages an earlier high beta range for young subjects and later low beta frequency range also includes, but the beta desynchronization is more pronounced with progressing age. The appearance of between-group β2 differences close to task end may correspond to different extents of beta rebound response with increasing age. The beta rebound effect may reflect an age-dependent inhibitory process of the primary motor cortex (Gaetz et al. 2010) and this decreased motor inhibition may facilitate neuronal plasticity and promote motor learning. Post-movement beta synchronization was also interpreted as a correlate of 'idling' motor cortex neurons (Pfurtscheller et al. 1996) with progressive age.

During the cognitive processing, γ1 activity diminished with age, except for increased left frontal γ1 activity for high-frequency tone stimulation (non-dominant reaction) and right occipitoparietal γ1 activity for low-frequency tone stimulation (dominant reaction). During cognitive processing, induced γ1 oscillations appeared in different post-stimulus intervals and their functional role relates to a 'large-scale integrated' process, which by transient

synchronization between spatially distributed neural assemblies, processing distinct features, should enable a coherent behavior and cognition (Donoghue et al. 1998, Varela et al. 2001). Through the comparison of auditory choice reactions, induced γ1 was enhanced by selective attention (Tallon-Baudry and Bertrand 1999). This effect was most prominent over the frontal and central scalp areas (Tiitinen et al. 1993). During cognitive processing, γ1 oscillations were further linked to mechanisms of sensory information matching with memory contents (Kaiser et al. 2009a, 2009b, Dushanova 2011), acquisition and retention of relevant stimulus features in memory (Karakas and Basar 1998, Dushanova 2011), and to post-discrimination processes related to the late cognitive P3 wave (Basar et al. 1993). Greater γ1 decrease in the elderly group could reflect less efficiency in a spatially localized gamma-band network specifically involved in auditory short-term memory to attain mental representation of the specific tone stimulation in order to correct tone discrimination and avoid wrong hand reaction and this process could be affected by age (Kaiser et al., 2009a, 2009b). Thus, the enhancement of left frontal γ1 responses to high-frequency tone stimulation and right occipitoparietal responses to low-frequency tone stimulation (100–800 ms after stimulus onset) in the elderly group may be associated with a compensatory function of these brain areas for increased attentional level to memorize stimuli. Correlations between gamma1 activity and performance have been seen only after high tone stimulation (Jokeit and Makeig 1994, Kaiser et al. 2009a, 2009b). Fast- and slow left-hand reacting subjects exhibit different patterns of gamma1 band activity when responding as quickly as possible to high-frequency auditory stimuli. A more sustained gamma1 representation of the memorized information has been shown at the parietal sites in the young group and at a left frontal side in the elderly group, but increased γ1 activity in elderly subjects was shifted from posterior to anterior sides at the task end (650-800 ms after high-tone stimulus onset).

During early cognitive processing, high-frequency tone perception evoked larger whole-head γ2 response in the elderly group. The parietal areas also appear to be more strongly involved in late cognitive processing with increasing age, which may be related to different levels of effort in "high-level cognitive processes" (Pantev 1995, Tallon-Baudry and Bertrand 1999, Pulvermüller et al. 1997, Miltner et al. 1999). The γ2 showed opposite between-groups amplitude relations. The slow γ2 wave responses, observed only in the elderly group, accomplished by an activation or reactivation of the brain regions, maintained by the sensory representation regions and the activation of executive networks, reflect variations in memory load and are topographically distinct from more posterior activations for low tone stimulation to more anterior for high tone stimulation.

Only the elderly group presented significantly different high-frequency activity with regard to tone types. With progressing age, motor task difficulty (higher for low-tone stimulation and dominant hand reaction) affected the attentional level and may lead to less prominent movement-related β band desynchronization on the right sensorimotor area, more widespread effect on right parietal and centro-parietal areas in β2 sub-band and at the left temporal side in β1 sub-band (400–460 ms after stimulus onset). In spite of this, more expressed movement-related β2 desynchronization (after low-tone stimulation and dominant hand reaction) over the left frontal side and an increased fronto-central β1 activity after right hand movement execution showed that frontal executive networks are effective in maintaining the vigilance and attentional processes or may have a compensatory role on account of the functioning of the alerting network relevant to task difficulty.

The task difficulty (low tone stimulation/dominant hand reaction) could reduce parieto-central γ1 activity during cognitive processing due to attentional shift from a high tone stimulus to left hand reaction, which could be linked either to retention of the adequate stimulus in memory or post-stimulus discrimination processing related to the working memory. With increasing age, the higher frontal γ2 wave responses to high tone stimulations (than to low tone) showed that frontal brain areas might become more sensitive to a high-frequency tone (or tone frequency differences) and might influence sensory and cognitive processes related to tone discrimination and hand reaction choice, reflect short-term memory variations and late engaged more posterior sides.

CONCLUSION

Increased age caused reduced β1 activity irrespective of task requirements (left or right-hand movement) during cognitive processing. This difference shifted in fronto-parietal direction more expressed after a high-frequency tone. Periods of significant between-group β1 differences and their topographical distribution were specifically dependent on the task requirements. β2 modulation depended on tone and age, and was characterized by reduced regional-process specificity with progressing age during sensory, but not during cognitive processing. Beta2 and gamma activity were more pronounced with progressive age during sensory processing but reduced by age on cognitive processes. Only elderly subjects showed higher sensory frontal γ1 activity. Late cognitive γ2 changes were shifted from posterior to anterior brain regions with advancing age. With increasing age, the larger γ2 differences were more expressed over the frontal brain areas to tone

discrimination and hand reaction choice, reflected short-term memory variations. The influence of aging was higher on cognitive processes than on perceptual ones. The approach can be useful for practical clinical aims due to the prolonged life expectancy of the human population and the consequent need of an early discrimination between normal and pathological brain aging for early treatment of cognitive alterations and dementia.

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