ARTICLE IN PRESS

Clinical Neurophysiology xxx (2009) xxx–xxx

Contents lists available at ScienceDirect

Clinical Neurophysiology

journal homepage: www.elsevier.com/locate/clinph

Two discrete components of the 20 Hz steady-state response are distinguished through the modulation of activation level

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ARTICLE INFO

Article history:
Accepted 28 February 2009
Available online xxxx

Keywords:
Steady-state response
Auditory
Multi-way matrix factorization
Activation

ABSTRACT

Objective: To investigate the modulation of amplitude and phase precision of the auditory steady-state response (SSR) to 20 Hz stimulation in two conditions varying in the level of activation.
Methods: Click stimuli (20 Hz) were applied while subjects were sitting upright silently reading a book of interest (high activation level) and while subjects were sitting in a reclined position with eyes closed and the lights turned off (low activation level). Sixty-one channel EEG data was wavelet transformed, the amplitude and phase precision measures extracted and decomposed by the multi-subject non-negative multi-way factorization (NMWF).
Results: The NMWF decomposition of amplitude and phase precision measures resulted in the observation of two distinct components: a component at the frequency of stimulation – 20 Hz SSR and a component emerging at 40 Hz – 20 Hz SSR-related 40 Hz activity. Modulation by the activation level was observed only for 20 Hz SSR-related 40 Hz activity as increased amplitude and phase precision during low activation level. No such effects were observed for 20 Hz SSR.
Conclusion: The discrete components of the 20 Hz SSR are distinguished through modulation of activation level, 20 Hz SSR- related 40 Hz being higher in low activation state.
Significance: The biological modulation of 20 Hz SSR-related 40 Hz activity by the level of activation points to a physiological nature of this activity beyond a mere periodic effect in relation to the 20 Hz activity.

1. Introduction

The steady-state response (SSR) is observed when stimuli are presented periodically resulting in electroencephalographic (EEG) entrainment (Picton et al., 2003). Although, the nature of steady-state response (SSR) is unknown, it has been used as an index of the ability to generate particular frequencies in local cortical networks (Kwon et al., 1999; Light et al., 2006). The 40 Hz SSR has received most attention: it has been shown to be reduced both in schizophrenia and bipolar disorder, and in healthy subjects it is modulated by the attention and the level of activation (Griskova et al., 2007; Kwon et al., 1999; Light et al., 2006; O'Donnell et al., 2004; Pockett and Tan, 2002; Ross et al., 2004; Santarelli et al., 1995; Skosnik et al., 2007). Occasionally, stimulation at lower frequencies (i.e. 20 Hz) is used. An additional activity around 40 Hz in response to 20 Hz stimulation was reported and explained as a harmonic of the 20 Hz activity (Kwon et al., 1999; Pastor et al., 2002; Skosnik et al., 2006; Spencer et al., 2008). However recently Spencer et al. (2008) showed impaired 40 Hz harmonic in schizophrenic patients whereas 20 Hz SSR was not affected (Spencer et al., 2008). A more detailed analysis of the 20 Hz response might be helpful in elucidating the nature of SSRs, as 20 Hz is a frequency that stands in the middle of frequency range that either elicits transient responses (for example 10 Hz) or steady-state responses (for example 40 Hz). Previously, applying wavelet transform and recently proposed multi-subject non-negative multi-way factorization (NMWF) decomposition, we showed that 40 Hz SSR is stronger and more precise during a low arousal (resting closed eyes) condition as compared to the high arousal (upright reading) condition (Griskova et al., 2007). The terms of arousal and activation are often used interchangeably. However, as proposed by Barry et al. (2005, 2007), these terms reflect different aspects, arousal being a measure of the current energetic level of the organism and

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doi:10.1016/j.clinph.2009.02.175

activation being a separable tonic measure reflecting the task-related mobilization of energy (relative to some baseline level of arousal) to perform a task (Barry et al., 2005; Barry et al., 2007). In the current paper we analyze the effects of activation level on 20 Hz SSR, hypothesizing that it will show the same modulation pattern as 40 Hz SSR, i.e. Steady-state response would be larger and more precise in the low activation level condition as compared to high activation level condition.

2. Methods

2.1. Subjects

Eleven healthy subjects (six females) were included into the study. Written informed consent was obtained, as approved by the Ethics Committee, and the subjects were paid for the participation. Due to technical reasons, data of two subjects could not be used. The final sample consisted of nine subjects (four females). The mean age of the sample was 23.1 years (standard deviation (SD) 1.6).

2.2. Stimulation

A stimulus train lasted 1 s and consisted of 20 identical clicks each being identical 1.5 ms burst of white noise. The stimuli were delivered through Sennheiser HD 565 Ovation© headphones at peak SPL of 60 dB. Seventy-two presentations of the 20 Hz train were interspersed with trains of other frequencies (8, 10, 12, 30, 46 and 60 Hz not reported here, 40 Hz reported in Griskova et al. (2007)) with an inter-train interval of 1 s. Two runs lasting 22 min were recorded in each of two conditions used. Conditions were defined as follows: "high activation" condition when subject was sitting upright and reading a self-selected book (the attention to reading was not controlled); "low activation" condition when subject was sitting much reclined with closed eyes and the lights turned down. In general, the instruction given to the subjects was to let their thoughts wander and not pay attention to the stimulation. The order of stimulation conditions was not counterbalanced across subjects.

2.3. EEG recordings

EEG was recorded with 61 scalp electrodes (BioSemi Active electrodes system) arranged according to the International 10–10 system. Digitally linked earlobe electrodes were used as reference. The active recording reference electrodes (CMS-DRL) were placed centrally, close to POz. Data was recorded continuously at 2048 Hz/channel and band passed at 0.1–760 Hz by a LabView© application (ActivView©) on a Windows© based PC.

2.4. Data analysis

Off-line processing was performed in ERPWAVELAB and EEGLAB for MatLab© (Delorme and Makeig, 2004; Morup et al., 2007). Wavelet transformation (WT; complex Morlet wavelet from MatLab© Wavelet Toolbox; frequencies represented from 4 to 70 Hz, 2 Hz intervals between each frequency) was performed. This yields both the wavelet transformed evoked potential measure (avWT, corresponding to phase-synchronized WT amplitude measure) and phase synchronization index (inter-trial phase coherence, ITPC), that is best conceptualized as phase precision or synchronization of the evoked oscillations from trial to trial ranging from 0 (random phase) to 1 (nearly identical phase) (Morup et al., 2006). These measures describe evoked activity dealing with different domains of the signal – amplitude and phase – that allows more detailed description of the response. Additionally, WTav representing the average amplitude of the oscillation (both non-phase-locked and phase-locked) was investigated to obtain a measure of the total intensity increase induced by the stimuli and to check the possible confounding of the signal by muscular noise. Prior to WT, 15% of the epochs with the largest variability were rejected automatically. Individual time-frequency representation of avWT, ITPC and WTav across all channels was created. Following that the avWTs, ITPCs and WTavs were decomposed through non-negative multi-way factorization (NMWF) (Morup et al., 2006; Morup et al., 2007).

The application of NMWF creates time-frequency plots of the avWT and ITPC while indicating how the parameter varies with experimental manipulation. In other words, the multi-subject NMWF analysis of the 3-way array of channel × time-frequency × subject – condition gives the subject-specific strength to the activity that is most common across subjects, conditions and runs, i.e. creates a subjects-weighted collapse and makes it possible to quantify (by giving the single estimation of the measure of interest) how the measure of interest varies with experimental manipulation for all the subjects in all conditions (Morup et al., 2006; Morup et al., 2007). This has proven being useful in the analysis of event-related potentials (Arnfred et al., 2007; Arnfred et al., 2008). Prior to NMWF analysis, random avWT and ITPC activity, estimated by calculating the mean of an artificially generated random avWT and ITPC samples, was extracted (Morup et al., 2006). The primer window for mathematical decomposition was set as 10–70 Hz and −500 to +1500 ms. As explained in the results section, further analyses were performed on more narrow time-frequency windows to focus on beta and gamma range activities separately: for beta range analysis a window of 16–26 Hz and −10 to +1200 ms was used; for gamma range analysis a window of 30–46 Hz and −10 to +1200 ms was selected.

Grand averaged evoked potentials of SSR for both conditions were created (individual averages based on 122 epochs, referenced to digitally linked earlobes, cut into epochs (−500 to +1500 ms), filtered band pass 10–50 Hz).

Baseline EEG theta (4–7 Hz), alpha (8–12 Hz) and beta (13–30) power was measured for nine regions through the fast Fourier transformation of the 1000 ms inter-trial interval of each trial to assess the level of activation: left frontal (F3, F5), midline frontal (Fz), right frontal (F4, F6), left central (C3, C5), midline central (Cz), right central (C4, C6), left posterior (P3, P5), midline posterior (Pz) and right posterior (P4, P6). Subjects were observed during the experiment and interviewed about their state of activation after it.

The results of the NMWF decompositions were normally distributed (as indicated by Shapiro–Wilk test) and were further tested in repeated measures analysis of variance (r.m. ANOVA) (SPSS© v. 9.1) for effects of "condition", "run" and "condition * run" interaction. Baseline power measures were tested by r.m. ANOVA for effects of "condition" and "region" and "condition * region" interaction.

3. Results

SSRs were detected for all subjects in both conditions. The topographical representation of grand averaged steady-state evoked potentials is given in Fig. 1A and enlarged SSRs from Fz electrode for low activation and high activation conditions are presented in Fig. 1B.

The NMWF decomposition of avWTs and ITPCs resulted in the observation of two distinct components: a component at the frequency of stimulation (in the following named 20 Hz SSR) and a component emerging at 40 Hz (named 20 Hz SSR-related 40 Hz activity). Full range time-frequency plots of SSR as a weighted col-

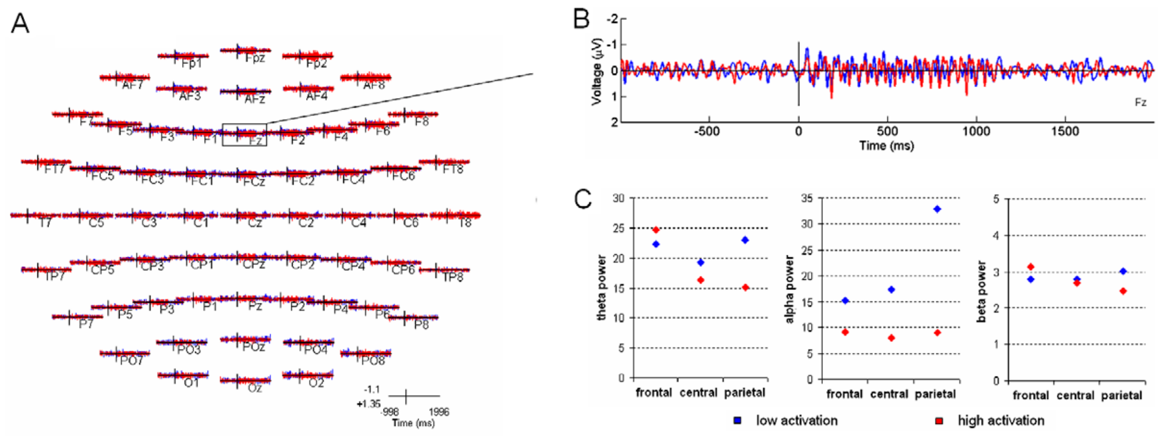

Fig. 1. The topological representation of grand averaged ERPs in low and high activation conditions is presented in (A). Enlarged ERPs for both experimental conditions from Fz electrode are depicted in (B) ($N = 9$; individual averages based on 122 epochs). (C) Powers of theta, alpha and beta bands averaged for frontal, central and parietal regions are presented. Alpha power significantly differed between two experimental conditions ($p < 0.05$).

lapse (relative weighting strength is given by the subject scores) across subjects, electrodes and conditions are presented in Fig. 2A and D. As the detected components were not separated by the decomposition, each subcomponent was separately analyzed in a narrowed time-frequency window.

4. NMWF scores of avWT, ITPC and WTav

4.1. 20 Hz SSR

As assessed by r.m. ANOVA, neither run nor condition (level of activation) had significant effects on avWTs and ITPCs of 20 Hz SSR ($F_{1,8} = 1.018$, $p = 0.343$ and $F_{1,8} = 0.681$, $p = 0.433$, respectively) (Fig. 2B and E). There was no interaction of the factors observed. There was a trend for higher WTavs of 20 Hz SSR in high activation condition (Fig. 3), however it did not reach statistical significance ($F_{1,8} = 4.719$, $p = 0.062$). The effect of run and the interaction of analyzed factors were not significant.

4.2. 20 Hz SSR-related 40 Hz activity

The r.m. ANOVA indicated significant difference between two conditions for both avWTs and ITPCs of 20 Hz SSR-related 40 Hz activity ($F_{1,8} = 7.970$, $p = 0.022$ and $F_{1,8} = 5,941$, $p = 0.041$, respec-

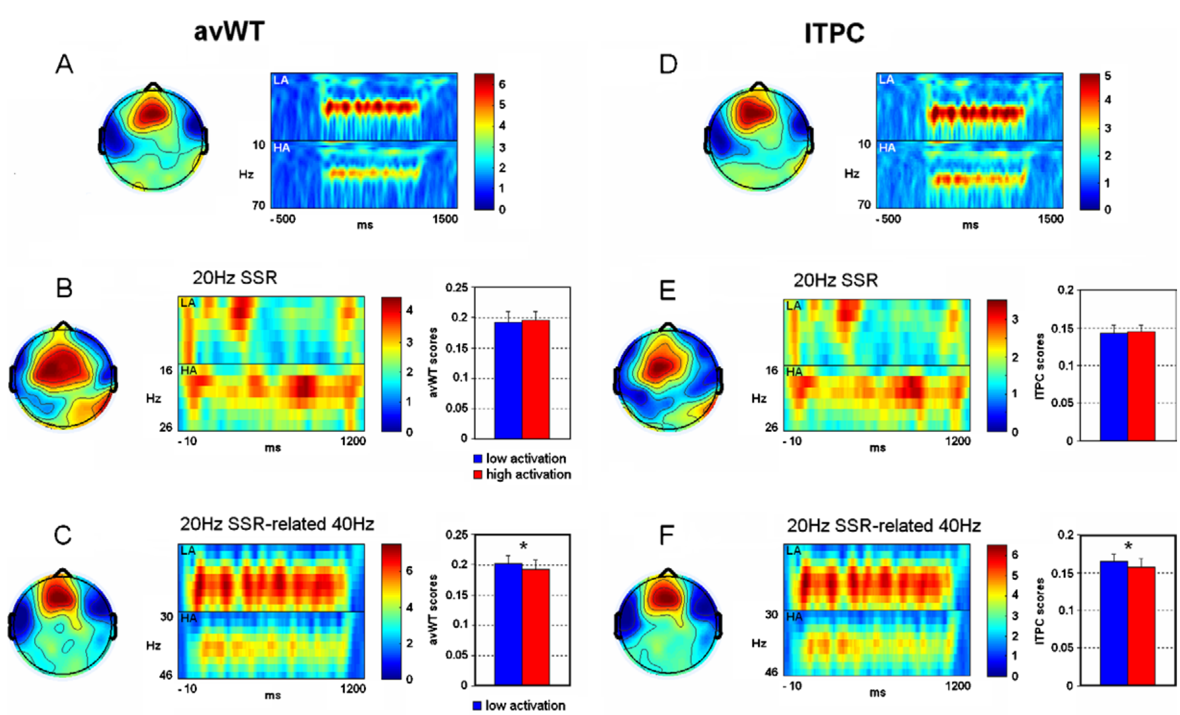

Fig. 2. Headplots and time-frequency plots (10–70 Hz, −500 to 1500 ms window) of avWT (A) and ITPC (D) as a weighted collapse across subjects and electrodes for the SSR in low activation (LA) and high activation (HA) conditions. Note appearance of pronounced activity around 40 Hz. Headplots and time-frequency plots of avWTs and ITPCs were created as a weighted collapse across subjects and electrodes for 20 Hz SSR (B and E) and for 20 Hz SSR-related 40 Hz activity (C and F) in both experimental conditions (LA – low activation, HA – high activation). As shown by means and standard deviations of the scores, avWTs and ITPCs of 20 Hz SSR did not differ between conditions whereas avWTs and ITPCs of 20 Hz SSR-related 40 Hz activity were higher during low activation condition ($p < 0.05$).

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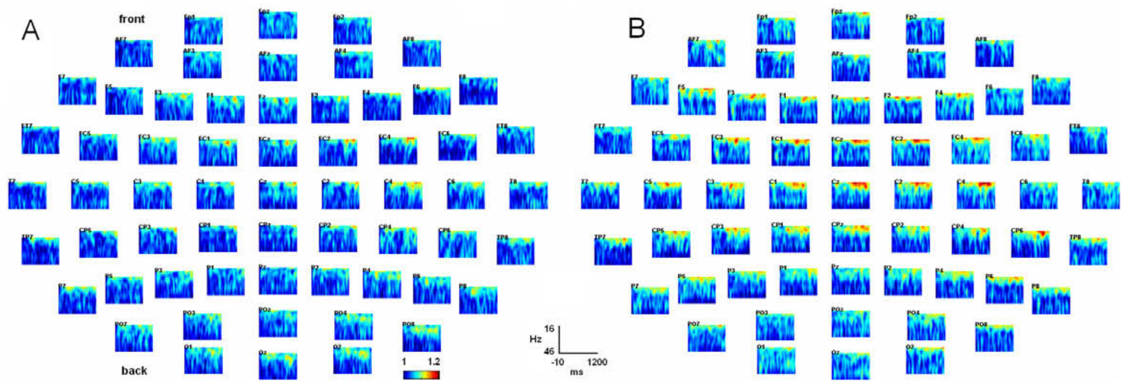

Fig. 3. Grand averaged time-frequency plots of 61 EEG channel in a topographical representation of WTav in low activation level (A) and high activation level (B) conditions. A trend towards higher 20 Hz activity in (B) compared to (A) is observed, see Section 3.

tively), higher scores being obtained in the low activation condition (Fig. 2C and F). No effect of run and interaction of run*condition factors emerged. There were no effects of either run or condition ($F_{1,8} = 1.357, p = 0.278$), as well as their interaction, observed for WTavs of 20 Hz SSR-related 40 Hz activity (Fig. 3).

4.3. Baseline theta, alpha and beta power

The r.m. ANOVA failed to demonstrate any significant effect of condition and region for theta power, but there was a trend for condition*region interaction to be significant ($F_{1,8} = 158.354, p = 0.061$), indicating higher frontal midline theta dominance in the high activation condition. Significant effect of condition on alpha power emerged ($F_{1,8} = 13.310, p = 0.007$), alpha power being higher in the low activation state, but no effect of region and interaction of the factors was observed. Neither condition nor interaction of condition*region factors had an effect for beta power, meaning that beta power did not differ between conditions. However, a nearly significant effect of region was observed ($F_{1,8} = 181.789, p = 0.057$), pointing to larger beta power over right frontal area.

5. Discussion

Although the true nature of SSR is not known, this type of event-related potential is considered an index of the ability to generate particular frequencies in local cortical networks (Kwon et al., 1999; Light et al., 2006). Periodical 20 Hz stimulation leads to the electroencephalographic (EEG) entrainment (Fig. 1A) with a clear peak identifiable at 20 Hz in the power spectrum (Kwon et al., 1999; Pastor et al., 2002; Skosnik et al., 2006). However, conventional spectral analysis of 20 Hz SSR distinguished an additional peak at 40 Hz (Kwon et al., 1999; Pastor et al., 2002; Skosnik et al., 2006). The present time-frequency analysis of wavelet transformed 20 Hz SSR response also resulted in the identification of two components: a component within 20 Hz frequency range and a component peaking at 40 Hz (Fig. 1B). This time-frequency pattern of 20 Hz SSR was recently observed by Light et al. (2006) and Spencer et al. (2008) and it was presently distinguishable in both experimental conditions. Additional activity around 40 Hz in response to 20 Hz stimulation has previously been considered a harmonic of the signal (Kwon et al., 1999; Light et al., 2006; Pastor et al., 2002; Spencer et al., 2008). By definition, the harmonic is a single oscillation whose frequency is an integral multiple of the fundamental frequency (i.e. 40 Hz is a higher order harmonic of 20 Hz oscillation). However, several findings support the notion that 40 Hz activity elicited by 20 Hz stimulation is of physiological significance.

First of all, we have shown that phase locking and evoked amplitude of 20 Hz SSR-related 40 Hz activity were higher in the low activation state, whereas 20 Hz SSR did not differ between conditions. The latter is in line with Linden et al. (1985), who did not find any difference between aroused and sleep states in the amplitude and phase of 20 Hz SSR assessed by FFT but they did not evaluate 40 Hz activity (Linden et al., 1985). The divergent modulation of 20 Hz and 40 Hz activities is supported by the finding of Spencer et al. (2008), who demonstrated decreased phase locking and decreased evoked power of 40 Hz harmonic in the first episode psychosis, whereas 20 Hz SSR was not affected in their study (Spencer et al., 2008). In a report of SSR in schizophrenics and healthy subjects Light et al. (2006) did not find any difference in phase locking and evoked power of 20 Hz SSR (Light et al., 2006). Yet, they did not evaluate the 40 Hz harmonic, which is apparent in Fig. 3 of the report (Light et al., 2006). The figure shows that the 40 Hz harmonic is weaker in the schizophrenic patient group (Light et al., 2006). Secondly, the direction of modulation of 20 Hz SSR-related 40 Hz activity corresponds to our recent results on 40 Hz stimulation: we have shown increase of evoked amplitude and phase precision of the 40 Hz SSR during a low activation state compared to a high activation, reading condition (Griskova et al., 2007). Again, it corresponds to studies both by Light et al. (2006) and Spencer et al. (2008) where the impairment of 20Hz SSR-related 40 Hz activity in patient groups was of the same direction as the change in actual 40 Hz SSR (Light et al., 2006; Spencer et al., 2008).

Interestingly, the phase-locked 40 Hz activity was more prominent than 20 Hz activity in both experimental conditions in our study (Fig. 2A and D). The same relationship has been observed before as it is evident in the time-frequency maps both in Fig. 1 of Spencer et al. (2008) and Fig. 3 of Light et al. (2006): 20 Hz SSR-related 40 Hz activity is more pronounced than actual 20 Hz SSR.

Notably, significant modulation by the level of activation was apparent only for phase-locked activity (amplitude and phase), whereas no significant effects were obtained for total (both non-phase-locked and phase-locked) amplitude, although there was a trend for larger 20 Hz SSR amplitude in the high activation condition. In contrast to phase-locked measures, total amplitude of 20 Hz SSR was larger compared to 20 Hz SSR-related 40 Hz activity. This may be explained by slightly larger frontal beta power in the high activation level condition.

Finally, a slight difference in the topographies of the 20 Hz SSR and 20 Hz SSR-related 40 Hz activity is worth mentioning: 20 Hz SSR is more centrally located (maximum over FC1 electrode);

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whereas 20 Hz SSR-related 40 Hz activity has frontal topography being maximal over Fz electrode (Fig. 2). To statistically confirm this trend additional analyses are needed. However, to our knowledge there are no analyses techniques available to estimate topographical difference and perform source-location of phase-locked activity. Commonly, the difference in topographies is a sign of different generators (Michel et al., 1999). Whereas frontal-central topography (maxima over Fz, FCz or Cz) of 40Hz SSR is a widely accepted finding when binaural stimulation is used (Hong et al., 2004; Kwon et al., 1999; O'Donnell et al., 2004), however, no reports could be found on the topography of 20 Hz SSR.

Along with a globally higher alpha power in the low activation condition, we observed a slight trend for theta and beta powers to be larger over frontal region in the high activation level condition. The involvement of both theta and beta in reading has previously been shown: frontal theta and beta are increased during semantic task completion (Fitzgibbon et al., 2004; Spironelli et al., 2008). Taking into account the suggestion of Barry et al. (2005, 2007) that increase in arousal is marked by a global decrease in alpha, whereas the specific regional activity is associated with task processing (Barry et al., 2007; Barry et al., 2005) we speculate that both modulation of activation level together with change in arousal level following the current experimental manipulation was successful. The finding was also substantiated by the statements from all the subjects that they entered a relaxed state and felt sleepy during the low activation level- resting condition. Focal attention has been shown to cause increase of 40 Hz SSR. While Linden et al. (1987) failed to show any effect of attention on SSRs, a recent study by Ross et al. (2004) reported some increase of 40 Hz SSR during a focal attention (Linden et al., 1987; Ross et al., 2004). Skosnik et al. (2007) found that attention enhances power and phase locking of 40 Hz SSR, but both 20 Hz SSR and its 40 Hz harmonic did not change with the changing level of attention in their study (Skosnik et al., 2007). The general concept of these studies was either to ignore stimulation or to actively attend and respond to it, thus both conditions were in alert states. We assume that focal voluntary attention on the stimuli in our study is sparse due to the study design and the instructions given to the subjects. i.e. to let their thoughts wander and not pay attention to the stimulation. Likewise, the increased power of 20 Hz SSR-related 40 Hz activity in the low activation condition was not an effect of muscular noise, because WTav in the range of 30–46 Hz did not differ between the two conditions.

It is widely accepted that the gamma response serves a broad range of physiological functions: early phase-locked gamma being primarily a manifestation of sensory processing and late non-phase-locked gamma resembling cognitive processes (Karakas et al., 2001). It has been shown, that early sensory gamma response is modulated via top-down processes (Karakas and Basar, 1998; Karakas et al., 2006). Taking this into account, it was expected that the change in the level of activation would affect sensory gamma component of SSR. Speculatively, the higher level of gamma activity evoked in the closed eyes condition could be a manifestation of at least two separate processes: It could either be a manifestation of an increased focal cortical activity due to induced shifts of involuntary attention in the closed eyes condition or be a manifestation of a sensory cortical inhibition during the cognitive task of reading. The higher estimated values of avWT and ITPC of 20 Hz SSR-related 40 Hz activity in the current study, together with our previous report on higher avWT and ITPC measures in 40 Hz SSR suggest that the closed eyes condition might be of choice when different subject groups are examined for phase-locked gamma response differences.

The main limitations of the study are the small sample size (nine subjects) and the fact that the experimental conditions were not counterbalanced across the subjects. These issues should be addressed in future studies investigating the nature of SSR-related gamma activity.

Summing up, the biological modulation of 20 Hz SSR-related 40 Hz activity by the level of activation and disease, points to a physiological nature of this activity beyond a mere periodic effect in relation to the 20 Hz activity. The more pronounced level of expression of the 40 Hz activity as compared to 20 Hz SSR also supports this point. Future studies with larger sample sizes should focus on this difference and explore its physiological significance.

Acknowledgements

The study was financially supported by the Lundbeck Foundation, the Gangsted Foundation, the Novo Nordic Foundation, the Danish Research Council and Cirius.

We thank Sv. Christoffersen and Ch. Tarrild for stimulation apparatus and software development.

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